REPORT OF THE INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH PLANNING WORKSHOP

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EXECUTIVE SUMMARY

Concern for wildlife in the management of second growth stands on Vancouver Island has increased recently as more and more of the island comes under intensive silvicultural management. The heightened awareness of the problems of integrated management of forests and wildlife on Vancouver Island prompted the Ministeries of Forests and Environment to initiate a 5 year project, called the Integrated Wildlife-Intensive Forestry Research (IWIFR) program. To help plan the program, the Technical Working Group (TWG) of the IWIFR program sponsored a five day research planning workshop in North Vancouver, British Columbia during January 19-23, 1981. The workshop was conducted using the methodology of Adaptive Environmental Assessment and Management and had the following objectives:

(a) develop a framework for cooperation and communication between wildlife and forestry interests;

(b) develop a conceptual framework, in the guise of a computer simulation model, to use as a guide in developing a research plan for IWIFR;

(c) develop a set of hypotheses about important processes in the system under study;

(d) develop a framework for testing hypotheses, and provide a basis for evaluating the relative importance of different processes; and

(e) resolve the question of the level of detail for research in the program.

The focus of the workshop was the construction of a numerical simulation model which integrated the hypotheses of participants about important processes and dynamics of forestry and wildlife concerns. This report is a synthesis of workshop proceedings and subsequent model simulations and analysis and is therefore a guide for developing a research plan for IWIFR.

The building and analysis of the simulation model is used in the report to develop this research planning guide. The model is described in terms of its temporal and spatial characteristics and the important linkages between each of its component subsystems - vegetation, timber, deer, elk and predators. A detailed discussion of each of the submodels is then given. Particular attention is paid to the hypotheses implicit in the functional relationships that were developed at the workshop. Initial simulation results from a number of scenarios developed by the participants during the workshop are presented.

The actual process of constructing the simulation model during the workshop and examining its behavior revealed conceptual and information needs which represent deficiencies in understanding of the processes and dynamics of forests and wildlife. Identification of these needs is critical to the development of a research plan for IWIFR.

The results of research undertaken to meet these needs can be used as refinements to the existing submodels. These refinements require new conceptualization of parts of the existing model, addition of important components that were left out of the initial model, or the acquisition of better data. However, it is strongly recommended that a thorough analysis of the concepts and data used to develop the present model be conducted before any model

refinements are made. No refinements which add to model complexity should be made until the dynamics of the current version are well understood.

The conceptual deficiencies are restated as hypotheses about system processes and dynamics. Alternate hypotheses are stated and suggestions are given as to how the hypotheses may best be tested. Most of these are interdisciplinary in nature and span forestry and wildlife concerns. Therefore research on any of the hypotheses will benefit enormously from an interdisciplinary approach. The careful design of an experimental forest management plan to provide an arena for evaluating deer, elk and predator responses to a variety of management actions is encouraged.

ACKNOWLEDGEMENTS

We thank all the workshop participants for their cooperation and productive contribution to the success of this effort. In particular, Don Eastman and Rick Ellis of the Technical Working Group of the IWIFR Program assisted in coordinating and organizing the workshop. Their efforts are appreciated.

Many of the comments and criticisms by participants of the draft version of the report proved valuable in the analysis of ideas presented in parts 8 and 9. We felt that these comments were important enough to be included in an appendix to the report.

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1.0 INTRODUCTION

Concern for wildlife in the management of second-growth stands on Vancouver Island has increased recently as more and more of the island comes under intensive silvicultural management. The heightened awareness of the problems of integrated management of forests and wildlife on Vancouver Island prompted the Ministries of Forests and Environment to initiate a 5 year project, called the Integrated Wildlife-Intensive Forestry Research (IWIFR) program, for research on the effects of silvicultural practices in second-growth stands on wildlife populations.

Projects of this magnitude are inevitably difficult to design effectively. The scope of the IWIFR project touches on silviculture, forest ecology, wildlife biology, and socio-economic considerations and involves numerous agencies and individuals with particular perspectives, expectations, and biases. Although initially the research questions all seem relevant and important to answer, it is critical that the key research questions are identified early in the program. Careful structuring of the research plan becomes a necessity when research is being done under limited budgets in both money and time.

Simulation models are powerful tools for identifying critical research questions. The consequences of a large number of hypotheses and assumptions can be quickly examined and evaluated. The simulation modelling workshop, as part of the Adaptive Environmental Assessment Methodology (AEAM), is a useful mechanism to construct a simulation model of a resource system. It allows research specialists to formalize and explicitly state their understanding of the

system and its components, identify critical assumptions within each discipline, identify the interactions among subsystems, and identify important research questions within and among disciplines.

The Technical Working Group (TWG) of IWIFR sponsored a simulation modelling workshop in North Vancouver on January 20-24, 1981. The specific objectives of the workshop were to:

(a) develop a framework for cooperation and communication between wildlife and forestry interests;

(b) develop a conceptual framework, in the guise of a computer simulation model, to use as a guide in developing a research plan for IWIFR;

(c) develop a set of hypotheses about important processes in the system under study;

(d) develop a framework for testing hypotheses, and provide a basis for evaluating the relative importance of different processes; and

(e) resolve the question of the level of detail for research in the program.

It was agreed at the beginning of the workshop that elk, deer, and their predators would be the only wildlife species considered in the workshop.

1.1 AEAM Methodology

Traditionally, research programs concerned with resource management issues have attempted to fund as many projects as possible which appear to be important issues of concern. Little thought is given to coordination of research between disciplines or to critical evaluation of particular projects

in the light of the dynamics of other parts of the system. The result is a series of research experiments on very specific parts of a problem which have little or no relevance to other pieces of the system.

Over the last decade a tool popularly known as "the modelling workshop" has been developed by environmental scientists and systems analysts at the University of British Columbia and the International Institute for Applied Systems Analysis in Austria. The methodology overcomes many of traditional pitfalls of large interdisciplinary research programs (Holling, 1978).

The focus of a simulation modelling workshop is to construct a quantitative dynamic simulation model of the system under study. The development of the simulation model forces the participants to view their areas of interest in the context of the whole system, thereby promoting interdisciplinary understanding of the system under study.

Simulation models require explicit information. In the workshop, specialists are forced to be precise about their assumptions. This objectivity exposes conceptual uncertainties about system behaviour and identifies research questions that are critical to investigate before the system dynamics can be accurately predicted.

The workshop is usually 5 days in length and proceeds roughly as follows. First, the problem and the system are clearly defined and bounded. This is done by stating the possible human interventions, or actions, which can be performed on the system and the measures of system performance, or indicators, which participants use to evaluate the consequences of actions. The model itself includes those processes which are required to translate

the actions to the indicators. The system is then temporally and spatially defined. The number and size of spatial units to be modelled and the number and length of time steps are defined. The system is then divided into 3 - 6 subsystems; these represent the major disciplinary concerns represented at the workshop. Each participant is assigned to a subgroup, each subgroup having the responsibility of developing a submodel of a specific subsystem.

Second, the information transfers among subsystems are defined. Each subgroup must explicitly state the information it requires to make predictions about how its subsystem will change in one time step. These information transfers represent specific hypotheses about how the dynamics of particular parts of the system are related to the dynamics of other parts of the system. It is during this exercise, known as "looking outward", that interdisciplinary communication becomes essential.

Third, the submodels for each subsystem are constructed. Each subgroup must conceptualize the processes needed to predict the relevant indicators and information requested by other subgroups, given the relevant actions and information they have requested from other subgroups.

Fourth, the submodels are linked together into the full simulation model. The complete model is "run" under a variety of scenarios to explore the consequences of various hypotheses about system structure. This exercise defines critical hypotheses (and therefore research priorities) which must be tested to improve the collective understanding of the system. The workshop concludes with a discussion of the preceding days' activities.

2.0 BOUNDING THE IWIFR SIMULATION MODEL

IWIFR is a research program charged with improving the understanding and prediction of wildlife responses to silvicultural manipulations of second-growth forests. To this end, description of the feasible management alternatives, or actions, and the measures used to evaluate the effects of actions on the bio-physical system, or indicators, begin to describe the realistic limits of the system which will be considered during the workshop. The system to be simulated is further defined by placing the actions and indicators in a manageable spatial and temporal framework.

2.1 Actions

Actions, in the context of the IWIFR programs, are the feasible human interventions which can alter the characteristics of second-growth forests and wildlife populations. It is important to define the actions as single interventions (e.g., scarification) rather than multiple, or a class of, interventions (e.g., site preparation). Particular components of the system may respond differently to specific actions which are often grouped into one generic category.

During the workshop forest-related actions fell into a few sets which tended to be applied at particular stages of forest development, while wildlife-related actions could be grouped into the broad categories of enhancement and control (Table 2.1). In addition, there were a series of possible actions suggested by participants which would not directly manipulate the forest or wildlife but could influence the dynamics of both.

2.2 Indicators

Indicators are those measurements which individuals use to evaluate the state, or health, of a system. They are the links between the simulation model and the participants' "mental" model of the system. Different people use different measures of system performance and it is therefore important to compile a comprehensive set of indicators that represent the interests of all participating agencies and groups. This ensures that the simulation model remains relevant to the concerns of all participants.

The indicator list generated at the workshop reflected the two major areas of focus - forestry and wildlife (Table 2.2).

2.3 Space

The initial discussion of the spatial resolution of the model was straightforward. Participants felt a hypothetical watershed of 80 km^2 in area, divided into 100 equal-sized units of 80 hectares would be adequate to represent the spatial dynamics of relatively isolated populations of deer and elk, and could be used to realistically simulate forest management practices such as clear-cutting.

Difficulties arose later in the workshop when participants realized that the internal dynamics of a site could only be applied to the entire site. Factors such as micro-habitat differences in specific areas within a single site could not be considered.

The scope of any model, however, is a compromise between the specific, enabling examination of very specific hypotheses and the general, enabling examination of general

Table 2.1 List of actions developed at the IWIFR Workshop

I. Forest-Related

A. Harvesting

i. clear cut: cable
skidder
aerial

ii. selective*

iii. two pass

iv. shelterwood*

B. Establishment

i. site preparation: burning - spot*, broadcast
mechanical - scarification
weed control - mechanical*, chemical

ii. regeneration: artificial - seeding, planting, conversion*
natural

iii. weed tree control*: mechanical
chemical

iv. protection from destructive agents*

C. Tending

i. thinning: juvenile spacing
commercial thinning

ii. pruning*

iii. fertilization*

iv. protection from destructive agents*

II. Wildlife-Related

A. Enhancement

i. predator control

ii. winter feeding*

iii. enhance browse production*

iv. stock with animals

v. remove poaching*

B. Control

i. change bag limit

ii. change hunting season length*

iii. change number of hunting permits*

iv. change sex and age distribution of hunt

v. predator control

vi. repellents*

vii. animal removal

III. Other*

i. construct roads

ii. construct trails

iii. construct campsites

iv. alienate and extract land: urbanization
coal development
reservoir construction

*not implemented due to lack of time, information,
or infeasibility because of spatial and temporal scales

Table 2.2 List of indicators developed at the IWIFR Workshop

I. Forest-Related

i. volume (m^3/ha)
ii. stand density (stems/ha)
iii. piece size volume (m^3/tree)
iv. tree height (m)
v. % brush cover
vi. % crown cover
vii. mean annual increment (m^3/ha, m^3/stem)
viii. debris density
ix. rotation age
x. "wildlife site index"*

II. Wildlife-Related

i. number and distribution of elk (by age and sex class)
ii. number and distribution of deer (by age and sex class)
iii. age-specific birth rates
iv. body weight (kg)
v. antler size (score)*
vi. number killed by hunters
vii. calf to cow ratio
viii. additional mortality as a result of environmental factors*
ix. number of predators by predator type
x. seedling mortality from browsing (stems/ha)
xi. height growth reduction from browsing (m)

*not implemented.

N.B.: II iii-viii refer to elk and deer

classes of hypotheses. Given the objectives of the workshop, (Section 1) a broad perspective which would permit evaluation of the importance of various classes of hypotheses, such as predation versus food limitation in wildlife dynamics, was necessary. Participants recognized that the single model with one hundred 80 ha. sites developed at the workshop could not address hypotheses at every level of detail but could address general hypotheses at a broad scale.

2.4 Time

The time horizon of the model was agreed to be 2 forest rotations. This would mean a simulation length of 200 years on the poorest sites. Initially, forestry interests said that the dynamics of an established and growing forest were slow enough to allow a model iteration of 5 or 10 years. However, the interaction between the forest and wildlife, in terms of animal damage and population responses to changing habitat conditions, can occur on a faster time scale. Many of the plant species are annuals; others put on a flush of annual growth. Elk and deer have an annual cycle of mating, wintering, calving, and summer feeding. Yet, dispersal responses and processes of the wildlife occur over periods of time shorter than one year. It was decided to let the model have an annual time step and allow for implicit seasonal representation in the submodels if necessary. The wildlife submodels considered 3 seasons: winter (November - February), spring (March - May), and summer (June - October).

2.5 Submodel Definition

Having defined the spatial and temporal bounds of the model, as well as the key inputs and outputs, the system was divided into 5 subsystems. The criteria for proper division are: minimization of information transfers between subsystems (each submodel simulated a relatively isolated, self-contained part of the whole system), efficient division of the expertise of the participants such that each subsystem represents the concerns of a particular subgroup of specialists, and fairly equal programming workloads for each member of the workshop staff.

Participants agreed that deer, elk and predators were separate subsystems. The predator subgroup members were given the charge of deciding among themselves which types of predators to consider. Because hunters can "switch" from one ungulate species to another, the predator submodel was to consider the effects of hunting as well.

Participants also initially agreed to divide the biological habitat for wildlife according to the successional status of a site. Therefore, one subsystem was to have been "early" succession and another "late" succession. This concept was later abandoned because of the difficulty in defining biologically meaningful criteria for division and because the processes for predicting changes in habitat structure would have to be conceptualized twice. As an alternate, the biological habitat was divided into a subsystem which considered the dynamics of primary wood product species, called "timber" and a subsystem which considered the dynamics of other plants, called "vegetation".

2.6 Looking Outward

The purpose of looking outward is to define the pieces of information a particular subsystem requires from all other subsystems to predict how that subsystem will behave dynamically. This is a qualitatively different question than the traditional, which requires lists of "factors which affect" a particular component of a system. The product of this exercise is an interaction matrix, with the columns specifying what information a subsystem requires from each of the other subsystems listed on the rows (Table 2.3). The diagonals are crossed out because those represent the internal dynamics of each subsystem, a task left to the subgroups to consider.

We stress that each piece of information listed in the matrix represents a specific hypothesis. For example, the elk subgroup required from the timber subgroup debris height and cover. The hypothesis is that the presence and amount of debris has a significant effect on the ability of elk to distribute themselves.

2.7 Spatial, Site and Vegetation Characteristics

Considerable time was spent at the workshop in defining a minimum set of characteristics for each site. Again, there were tradeoffs to be considered, this time between spending a great deal of time describing the physical attributes of the hypothetical system and spending time considering the processes and hypotheses envisioned by participants as important in system dynamics. The general topographic and biogeoclimatic features of the region had to be derived by the participants and are given in Figure 2.1. The following characteristics had to be specified for each site and therefore derived by the

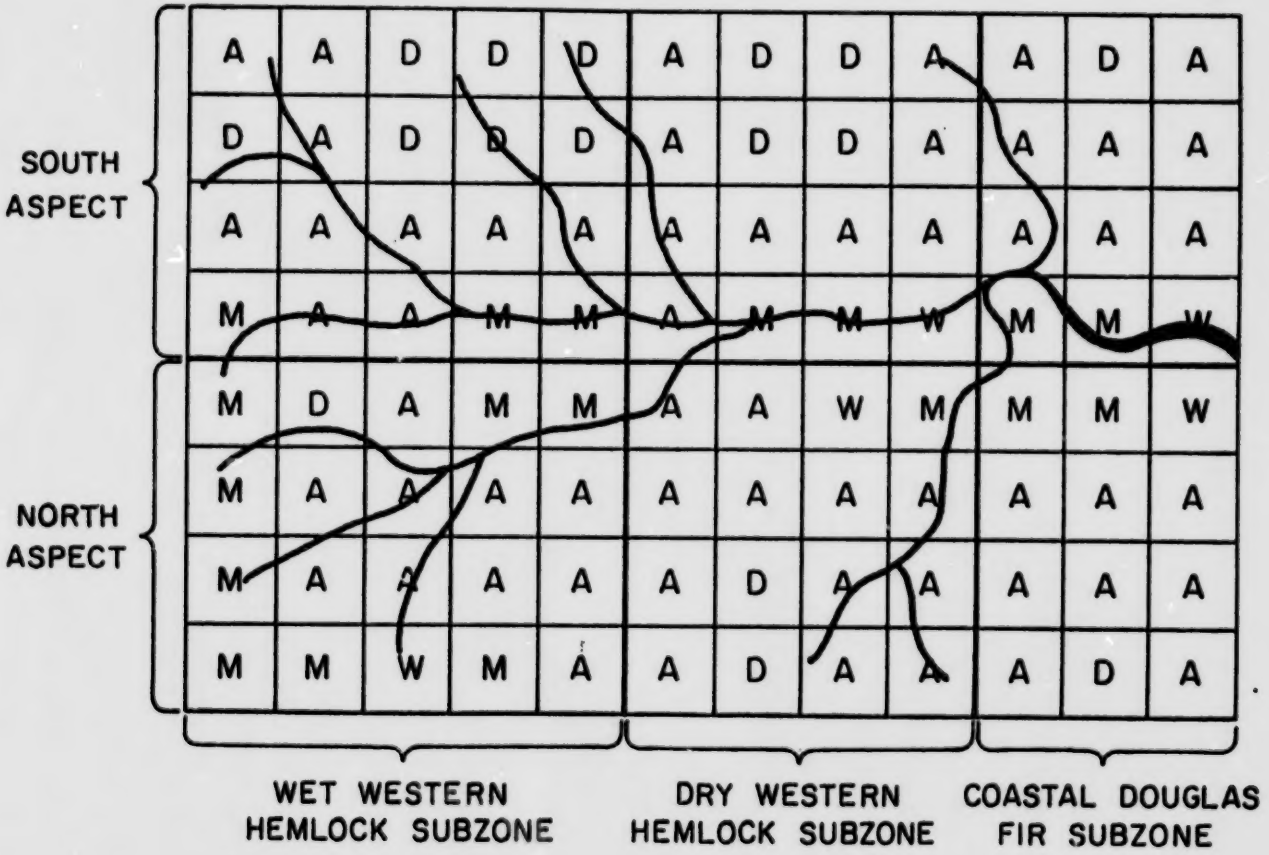
Table 2.3 Looking outward matrix for the LWIFR model

FROM \ TO	Vegetation	Wood	Elk	Deer	Predators
Veg.			biomass of forage by type (<2m)	biomass of forage by type (<2m) lichen litter fall	biomass of forage by type (<2m)
Wood	percent maximum possible crown biomass* % debris cover		% debris cover debris height stand density biomass of foliage (<2m) overstory height distribution of snow depths in time live crown ratio	% debris cover[1] debris height[1] stand density biomass of foliage (<2m) overstory height temporal distribution of snow depths live crown ratio[1]	stand density temporal distribution of snow depths foliage biomass (<2m)
Elk	forage biomass eaten by type	# stems killed[1] % leaders eaten[1] foliage biomass eaten		# elk[1] forage biomass[1] by type removed by elk	# elk by sex, age, season
Deer	forage biomass eaten by type	# stems killed[1] % leaders eaten[1] foliage biomass eaten	# deer[1] forage biomass[1] by type removed by deer		# deer by sex, age, season
Pred.			# elk killed by sex, age, season	# deer killed by sex, age, season	

*important information transfers not recognized during looking outward, but in subgroups

[1]not incorporated due to lack of information or time

Figure 2.1 General characterization of the hypothetical region.


SOUTH ASPECT
NORTH ASPECT
A A D D D A D D A A D A
D A D D D A D D A A A A
A A A A A A A A A A A A
M A A M M A M M W M M W
M D A M M A A W M M M W
M A A A A A A A A A A A
M A A A A A D A A A A A
M M W M A A D A A A D A
WET WESTERN HEMLOCK SUBZONE
DRY WESTERN HEMLOCK SUBZONE
COASTAL DOUGLAS FIR SUBZONE
MOISTURE TYPES : D — Dry
A — Average
M — Moist
W — Wet

participants to be able to simulate the model on the last day:

(a) stand age
(b) site index
(c) tending regime
(d) establishment regime (planting vs. natural)
(e) site preparation regime
(f) harvesting regime (harvest or no harvest)
(g) slope
(h) aspect

The dynamics of the following plant species were simulated:

Perennials -
(a) salmonberry
(b) elderberry
(c) willow
(d) salal
(e) huckleberry
(f) cedar

Annuals -
(g) skunk cabbage
(h) sword fern
(i) deer fern
(j) fireweed
(k) other "weeds"

(l) arboreal lichen
(m) Douglas fir
(n) western hemlock

The presence or absence of each plant on a site was a function of subzone and moisture regime.

3.0 VEGETATION SUBMODEL

The vegetation submodel was responsible for providing forage for the deer and elk subgroups, given relative crown biomass from the timber subgroup and previous feeding levels from the wildlife groups. The dynamics had to also be responsive to the forestry management practices simulated in the model.

A major conceptual problem with the submodel was defining the components of the vegetation to be simulated. Due to the limited time available in the workshop the subgroup was forced to compromise between gathering data to set initial conditions for the submodel and considering alternate hypotheses about vegetation dynamics and responses to feeding by wildlife. The subgroup finally decided to consider the dynamics of six perennial species, five types of annuals, and arboreal lichens. However the vast data requirements generated by this list of vegetation precluded inclusion of processes such as competition among the forage types.

3.1 Perennials

The six perennial species were assumed to grow logistically:

$$\text{biomass}_{t+1} = \text{biomass}_t + r * \text{biomass}_t \ (1-\text{biomass}_t/K)$$

where r is the intrinsic growth rate, K is the carrying capacity and biomass_t is the amount left after feeding by wildlife. The r and K parameters were estimated for each species in each moisture type and subzone (Tables 3.1 - 3.3).

Table 3.1 Vegetation parameters for coastal Douglas fir wet subzone, under conditions of no timber.

	Wet		Moist		Average		Dry	
Species	K	r	K	r	K	r	K	r
Salmonberry	6	2.0	17.5	3.0	0.4	1.5	0	-
Elderberry	1	2.0	2.5	2.5	0	-	0	-
Willow	1	1.2	1.25	1.2	0	-	0	-
Salal	0.5	1.2	1.25	1.2	5.6	1.5	4.8	1.5
Huckleberry	0.5	1.1	1.25	1.2	2	1.3	1.2	1.2
Cedar	1	1.1	1.25	1.1	0	-	0	-
Skunk Cabbage	0.05		0		0		0	
Sword Fern	0		1.1		0.005		0	
Deer Fern	0		0		0		0	
Fireweed	0		0.1		0.0225		0.00225	
Other Weeds	0.45		0.8		0.0225		0.00275	

K = Maximum Biomass (tonnes/ha) r = Growth rate

Table 3.2 Vegetation parameters for coastal western hemlock dry subzone, under conditions of no timber.

	Wet		Moist		Average		Dry	
Species	K	r	K	r	K	r	K	r
Salmonberry	6	2.0	13	3.0	1.0	1.4	0	-
Elderberry	1	2.0	2	2.5	0.5	1.3	0	-
Willow	1	1.2	1	1.2	0	-	0	-
Salal	0.5	1.2	1	1.2	6.0	1.6	4.0	1.7
Huckleberry	0.5	1.1	3	1.2	2.0	1.4	2.4	1.4
Cedar	1	1.1	1	1.1	0.5	1.1	1.6	-
Skunk Cabbage	0.05		0		0		0	
Sword Fern	0		1.25		0.005		0	
Deer Fern	0.025		0.13		0		0	
Fireweed	0		0.13		0.0225		0.00315	
Other Weeds	0.425		1.0		0.0225		0.00385	

K = maximum biomass (tonnes/ha) r = growth rate

Table 3.3 Vegetation parameters for coastal western hemlock wet subzone under conditions of no timber.

Species	Wet		Moist		Average		Dry	
	K	r	K	r	K	r	K	r
Salmonberry	6	2	9.35	2.5	0	0	0	0
Elderberry	1	2	1.7	2.2	0	0	0	0
Willow	1	1.2	0	1.2	0	0	0	0
Salal	.5	1.2	.85	1.2	3	1.1	7.7	1.1
Huckleberry	.5	1.1	5.1	1.2	7.8	1.6	1.1	1.3
Cedar	1	1.1	.85	1.1	1.2	1.1	2.2	1.1
Skunk Cabbage	.05		0		0		0	
Sword Fern	0		1		0		0	
Deer Fern	.025		.6		.005		0	
Fireweed	0		0		0		0	
Other Weeds	.425		.4		.045		.007	

K = maximum biomass (tonnes/ha) r = growth rate

3.2 Annuals

It was assumed that the biomass of each of the five groups of annuals was simply their carrying capacity (K). As with the perennials the carrying capacity was dependent on species, moisture and subzone.

3.3 Effect of Light Limitation on Carrying Capacity

The carrying capacity of both annuals and perennials was assumed to be a function of light penetration through the canopy formed by the timber species (Figure 3.1a, 3.1b). The surrogate for available light was taken to be the ratio of actual timber foliage to maximum possible timber foliage (Section 4.7).

3.4 Arboreal Lichens

Arboreal lichens begin growing in the forest after the canopy closure decreases, usually when tree maturity is reached. There was no convenient way to detect the reduction in crown closure given the present model structure. As an alternate, lichens were assumed to begin growing when the stand age reached 50. Lichen biomass was assumed to increase to a maximum biomass according to an annual growth rate. Both parameters (i.e., maximum biomass and annual growth rate) were dependent on subzone and moisture type (Table 3.4).

Thinning was assumed to reduce lichen biomass by the same proportion as the proportion of stems removed. Clear cutting eliminated lichens altogether.

Table 3.4 Parameters for arboreal lichen dynamics.

	North aspect		South apsect	
	K	years to K	K	years to K
CWHw				
dry	500	200	1800	100
average	200	250	500	150
moist	0	-	200	200
wet	0	-	0	-
CWHd				
dry	200	250	1200	130
average	0	-	200	200
moist	0	-	0	-
wet	0	-	0	-
CDFw				
dry	100	250	500	200
average	0	-	100	200
moist	0	-	0	-
wet	0	-	0	-

K = carrying capacity (kg/hectare)

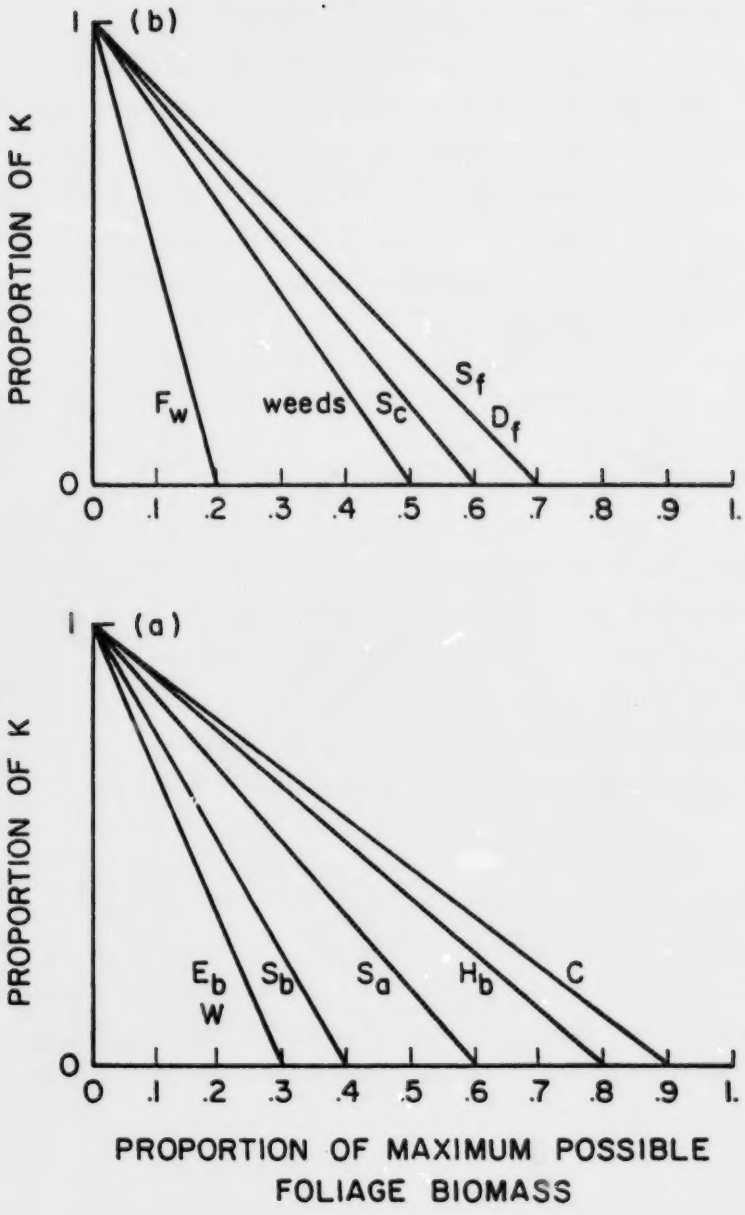


Figure 3.1 Effects of overstory biomass on vegetation carrying capacity. F_w = fireweed; S_c = skunk cabbage; S_f = sword fern; D_f = Deer fern; W = willow; E_b = Elderberry; S_b = Salmonberry; S_a = Salal; H_b = huckleberry; C = cedar.

3.5 Forage Available for Browsing

During the workshop there was considerable confusion over the amount of the forage species available as food for deer and elk. A decision was made to make 10% of the standing crop of both annuals and perennials and 13% of arboreal lichens available as food for deer and elk. This linear relationship is surely inaccurate and must be improved.

3.6 Effects of Site Preparation

Burning, scarification and herbicide application were implemented in the timber submodel. The effect of these actions was to reset the standing biomass of the vegetation species the year the trees were harvested, according to the type of site preparation and the response of each species to the different kinds of site preparation (Table 3.5). The biomasses were reset as a fraction of carrying capacity.

3.7 Fertilization

Fertilization could be specified by the user at any time in the simulation and was assumed to increase the carrying capacity of all perennials and annuals by 10% for 5 years.

Table 3.5 Effects of site preparation on vegetation. Site preparation was assumed to reset biomass of vegetation to percentages of carrying capacity for a given number of years.

Species	Burning		Scarification		Herbicides	
	% carrying capacity	# years	% carrying capacity	# years	% carrying capacity	# years
Perennials:						
Salmonberry	20	1	5	1	1	1
Elderberry	5	1	1	1	1	1
Willow	1	1	1	1	1	1
Salal	20	1	10	1	100	1
Huckleberry	20	1	5	1	5	1
Cedar	1	1	1	1	100	1
Annuals:						
Skunk Cabbage	-		110	7	-	
Sword Fern	-		110	7	-	
Deer Fern	-		110	7	-	
Fireweed	1000	10	110	7	-	
Other Weeds	-		110	7	-	

4.0 TIMBER SUBMODEL

The responsibilities of the timber subgroup were to produce a dynamic conceptualization of tree and forest growth, given a range of silvicultural actions and wildlife browsing levels. The submodel had to be responsive to an array of stand establishment and tending/harvesting regimes as well as wildlife browsing. It had to produce those variables which the other subgroups had identified as important information links in the looking outward exercise.

The possible actions for each site are given in Table 4.1; one action from each class was specified for each site. The various actions were hypothesized to have different consequences for development of other vegetation (Section 3) as well as debris levels and coverage.

The forest model considered each site as being even-aged and of a single species, either Douglas fir or western hemlock. State-dependent (as opposed to time-dependent) stand growth models exist for B.C. forests (e.g., Mitchell, 1975) but they are at an inappropriate level of resolution for the purposes of the workshop. Instead, a very simple representation of forest growth was constructed, taking care to ensure that the dynamics were responsive in a realistic manner to silvicultural practices and wildlife impacts. The basic driving variable for the submodel was the time since initiation of stand development (not the same as time since stocking), called "stand age". Participants felt that, for the purposes of the workshop the dynamics of both timber species could be regarded as the same. It was necessary to specify which species was growing on a site because of the differential feeding preferences of wildlife (Tables 5.4, 6.1).

Table 4.1 Management actions implemented in the timber submodel.

I. Site Preparation

i. nothing
ii. burn
iii. scarify
iv. herbicide

II. Regeneration	Stocking (/ha)	Initial Stand Age (yrs)
i. natural	500-1500	-3 to -7
ii. artificial	1500	0

III. Tending and Harvest	% Debris Cover	Debris Height (m)
i. space thinning	100	1.0
ii. commercial thinning	30	1.0
iii. clear cutting	50	0.5

4.1 Influence of Wildlife

Elk and deer were hypothesized to affect stem mortality and changes in growth.

4.1.1 Browsing Effects

4.1.1.1 Stem Mortality

The proportion of stems killed was assumed to be directly related to proportion of foliage eaten in a year, such that 50% of the stems were killed if 50% of the foliage was removed by wildlife. This relationship was assumed to be independent of tree age or size. The hypothesis implicit in this relationship is that the probability of death from browsing for an individual tree is linearly related to its relative foliage levels and independent of tree size.

4.1.1.2 Changes in Growth

Stand growth could be changed by browsing. The wildlife subgroups could not derive appropriate feeding relationships to calculate percentage of leaders eaten. The timber subgroup therefore hypothesized the relationship between percent leader loss and percent foliage eaten was that given in Figure 4.1a; this was then used to reduce stand age (Figure 4.1b). Note that, even if all leaders were eaten, stand age reduction would only be 0.9 years. The hypothesis implied in this relationship is that animal feeding can never completely halt stand development and that the stand can always eventually attain characteristics it would under conditions of no browsing. Tree characteristics are hypothesized to never be permanently altered by browsing.

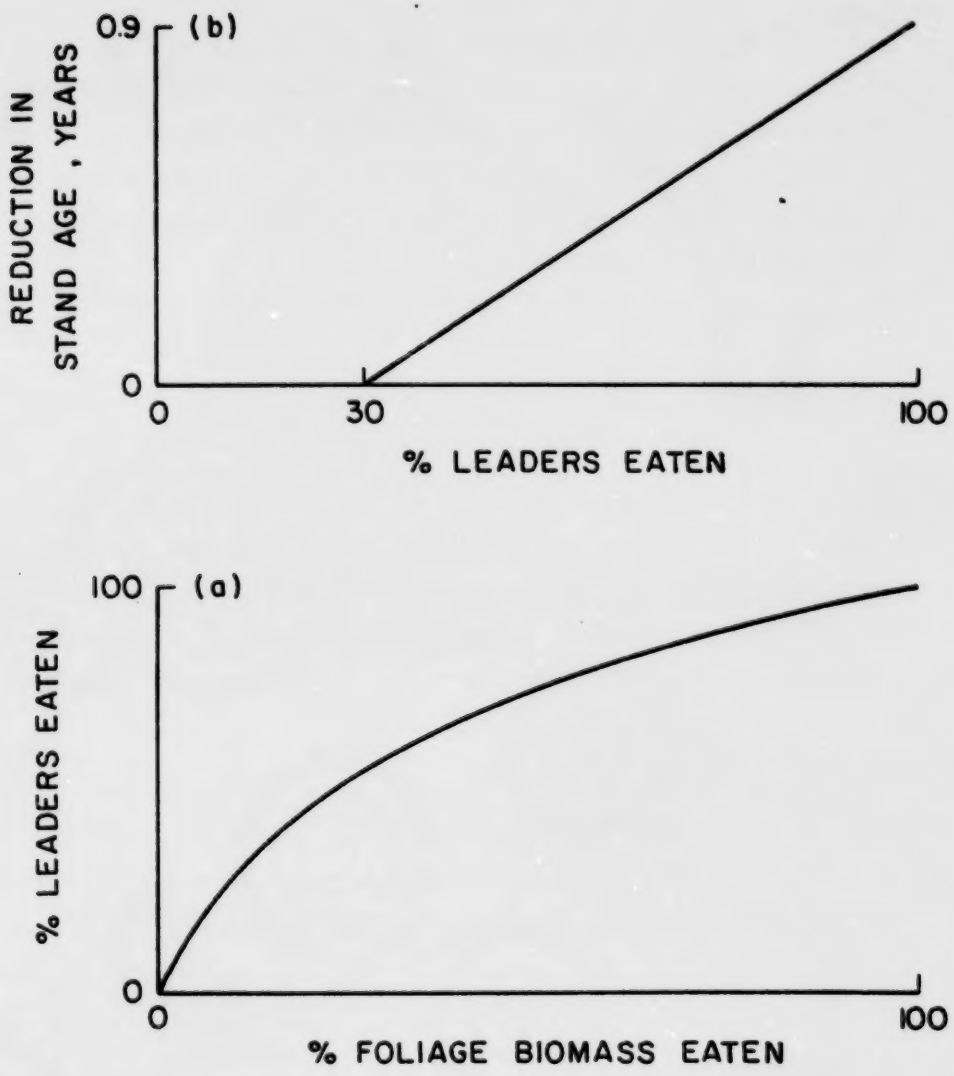


Figure 4.1 Effect of browsing on stand age.

4.1.2 Direct Influence

The wildlife subgroup could not derive appropriate relationships to calculate percentage of stems killed. There was considerable uncertainty in the direct effects of wildlife. It was assumed that the direct damage to the stand by deer and elk, such as trampling, was negligible and was not included in the model.

4.2 Height

Height growth was hypothesized to be a function of stand age and site index (Figure 4.2). Stand age was reset after clear cutting according to the regeneration policy (Table 4.1), incremented by 1 every simulated calendar year, and reduced by browsing (Section 4.1.1.2). Understory vegetation was assumed to not affect timber growth.

4.3 Timber Volume

Volume of timber was assumed to be a function of height and initial stocking (Figure 4.3).

4.4 Stand Density

Changes in stand density were hypothesized to be determined by natural mortality, spacing and thinning actions, and animal browsing (Section 4.1.1.1).

Natural mortality was applied to stems after removal from thinning and animal feeding. A natural decline in stand density was postulated (Figure 4.4) and the actual stand density was taken to be the density after thinning

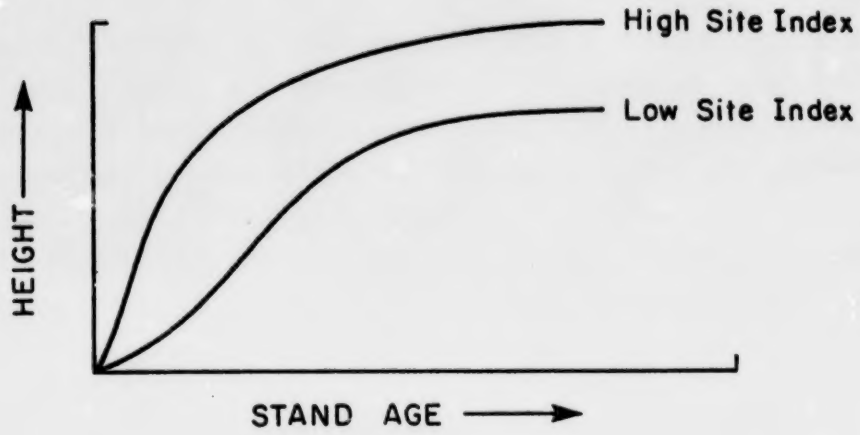


Figure 4.2 Stand height as a function of stand age.

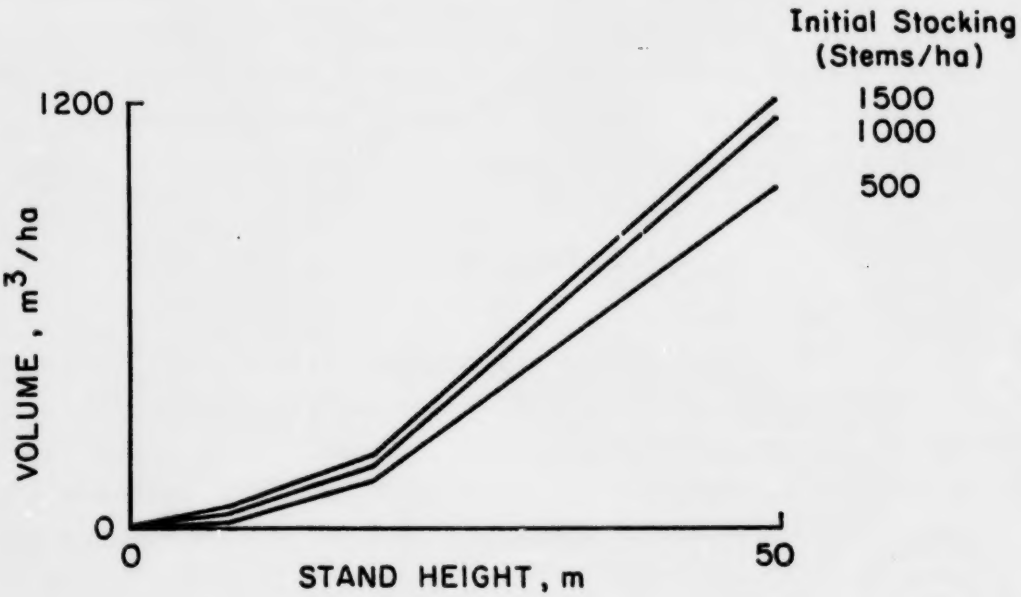


Figure 4.3 Stand volume.

and animal feeding or the density after thinning, animal feeding, and natural death, whichever was the lesser. Therefore, natural mortality immediately after a spacing is usually 0, until stand height becomes large enough. The stand was replanted if there were less than 700 stems/hectare at a stand age of 2 years and the stand had been established by planting.

4.5 Crown Closure

Crown closure was assumed to be a function of annual height increment and stem removal. It was assumed that there would be an added crown closure of 8% for every meter increment in stand height. Therefore, a stand becomes completely closed when the stand height becomes 12.5m. The crown opened as stems were removed by the combined effects of animal damage, spacing and/or thinning, and natural mortality (Figure 4.5).

4.6 Live Crown Ratio

Live crown ratio was assumed to be simply a function of stand height (Figure 4.6) with two of the interpolation points set by initial stocking. Maximum live crown ratio is therefore reached more rapidly in a high-stocked stand than in a low-stocked stand, reflecting the influence of intra-tree competition. Calculation of height to live crown was therefore:

height to live crown = height x (1-live crown ratio)

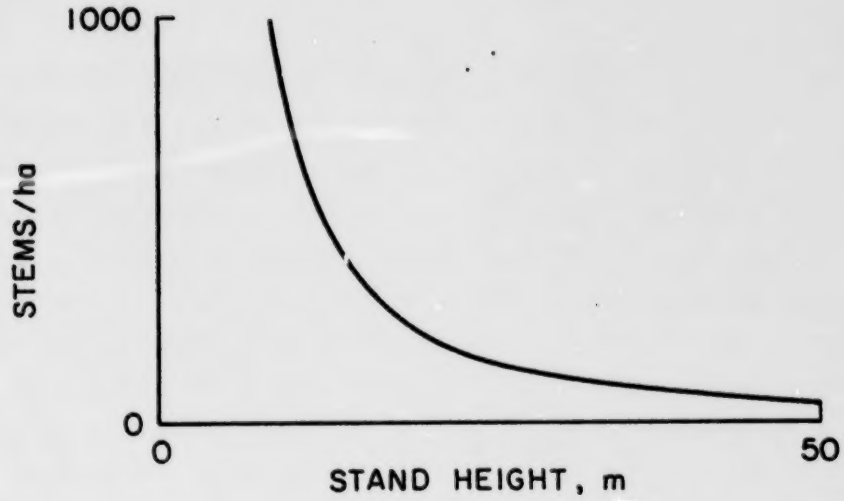


Figure 4.4 Natural stem mortality. Stand density is taken to be the stems left after all other mortality, or stems calculated from the curve below, whichever is lower.

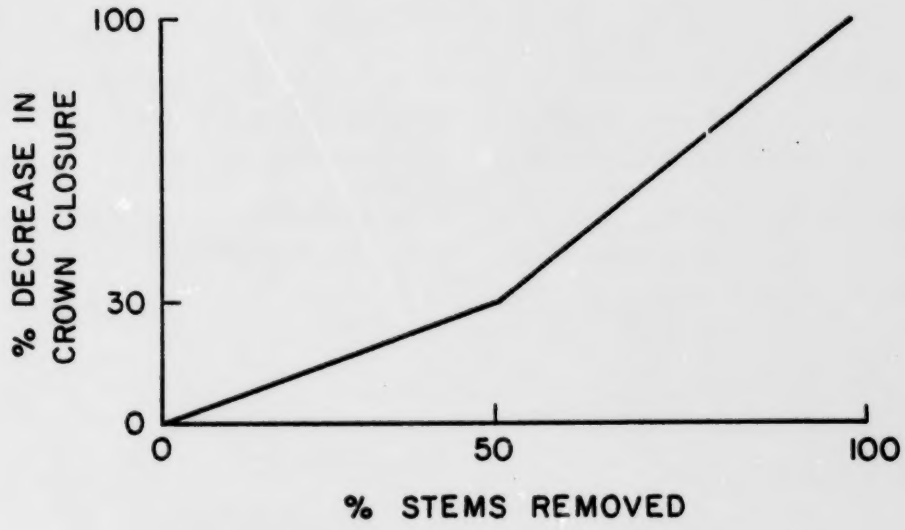


Figure 4.5 Effect of stem removal on crown closure. Stems can be removed by animal damage, silvicultural practices, and natural mortality.

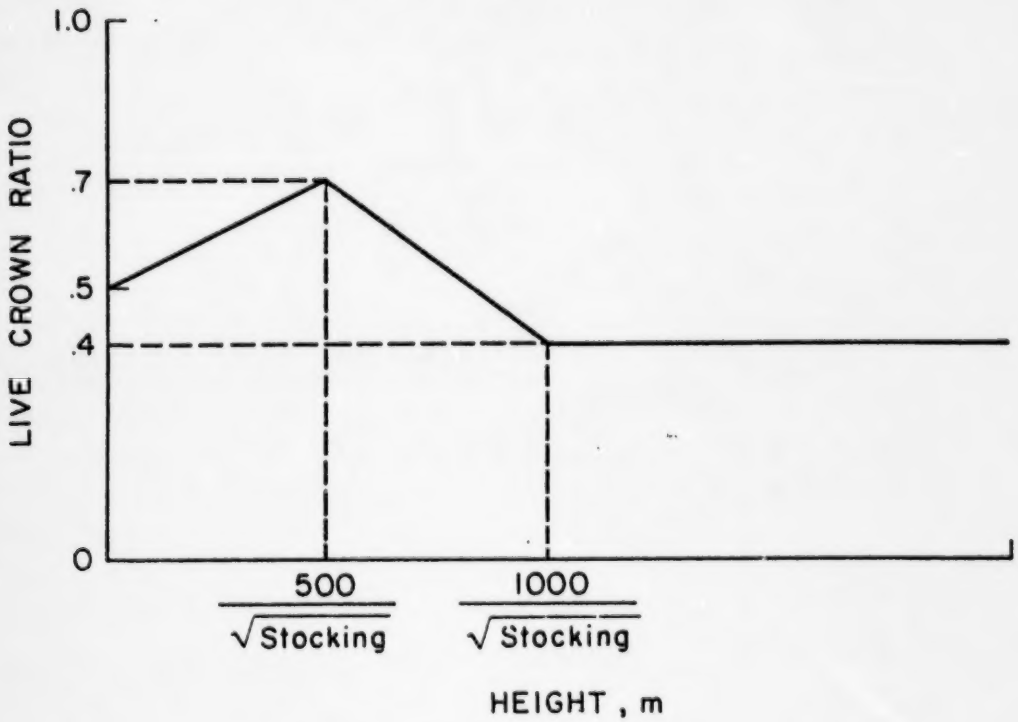


Figure 4.6 Live crown ratio.

4.7 Foliage Biomass Available to Wildlife

Tree foliage biomass regressions exist for B.C. forests (Kimmins, pers. comm.), but require knowledge of tree attributes other than those the model was calculating (such as diameter at breast height). Therefore, it was assumed that a tree produced a kilogram of foliage for every meter of crown length available to wildlife. The crown length available to wildlife was the live crown length if the height was less than 2m, 2m minus height to live crown if the height was greater than 2m and the height to live crown was less than 2m, or 0 if the height to live crown was greater than 2m.

The other vegetation subgroup requested proportion of maximum possible foliage biomass for the particular subzone to calculate stand closure effects on vegetation growth. A surrogate index used:

$$\frac{\text{stand height}}{\text{maximum stand height for subzone}} \times \text{(crown closure)}$$

This index reached 100% when stand height reached maximum and the overstory become completely closed.

5.0 DEER SUBMODEL

The general charge of the deer subgroup was to build a population model of black-tailed deer by developing a series of hypotheses specifying how the species responds to its environment. The group was specifically concerned with describing how the environment influences movement, feeding, survival and reproduction within the spatial structure described in Section 2.3. Much of this information was considered to be season specific; thus the functional relationships developed for these processes, or at least their parameters, were often different for the three seasons considered (Section 2.4).

Information provided by the deer subgroup to other groups included the number of deer in each age and sex class, the amount of food of each of the 14 types consumed over the entire year on each site (kg/ha) and an index of the quality of escape cover on each site.

The deer subgroup was also responsible for developing a model of winter snowfall for the area. The snow submodel will be described first, as it has important implications to some of the relationships discussed later in this section. It will be followed by a description of each of the processes mentioned above: movement, feeding, survival and reproduction.

5.1 Snowfall

5.1.1 Snow Reaching the Canopy

Snow was assumed to occur only in winter. To realistically represent natural temporal variation in snowfall patterns, the winter was divided into three distinct

periods. The potential snowfall depth in each period was allowed to vary (potential depth is defined as the depth of snow which would be on the ground if there were no canopy).

An additional component, not included in the model during the workshop but since incorporated, made the amount of snow reaching the canopy in the "middle subzone" 50% of that in the "upper" subzone and in the "low" subzone 10% of that in the "upper" subzone. The reduction factors attempt to mimic the geographical variation in snowfall.

The length of each period was also allowed to vary, provided that the sum of all three periods was always equal to the total length of the winter period (Section 2.4). These periods do not necessarily represent three consecutive periods of time. Rather, they represent a grouping of all days of winter into three classes corresponding to "low", "medium", and "high" snowfall. A key assumption here is that the effect of snowfall on the processes such as feeding and survival is independent of the sequence of snowfall events.

5.1.2 Snow Reaching the Ground

The actual depth of snow on the ground on a site was hypothesized to be a function of the depth of snow reaching the canopy and the effectiveness of that canopy at intercepting snow. The following relationship was defined to incorporate these two effects (Figure 5.1):

$$\begin{array}{l}\text{snow depth on site (i)} \\ \text{in winter period (j)}\end{array} = \begin{array}{l}\text{snow reaching} \\ \text{canopy on site} \\ \text{(i) in winter} \\ \text{period (j)}\end{array} \left[1 - \begin{array}{l}\text{crown closure} \\ \text{on site (i)}\end{array}\right]$$

Sites with trees less than two meters in height were assumed to have no interception capabilities. This relationship implies that a completely closed canopy will prevent any snow from reaching the ground, regardless of the amount of the snow reaching the canopy.

5.1.3 Food Covered by Snow

Having calculated the depth of snow on each site for each winter period, it was necessary to decide what proportion of food was unavailable to wildlife due to snow cover. Each food type was assigned to a height class and the proportion of food left uncovered in each class was defined by the following relationship:

$$\text{proportion uncovered on site (i)} = 1.0 - ESD * \text{depth of snow on site (i)}$$

where ESD is the height class specific slope of this relationship (Table 5.1). This slope increases as the height of the plant decreases making smaller plants unavailable at relatively small snow depth.

Special consideration had to be given to lichens. It was assumed that the amount of snowfall reaching the canopy in a particular snowfall period would reflect the intensity of snowfall during that period. It was assumed that the proportion of total lichens on the ground actually available for feeding upon would decrease as the amount of snow reaching the canopy increased (Figure 5.3).

Table 5.1 Slopes of the snow depth - food coverage relationship.

Food Type	Slope
salmonberry	.01
elderberry	.01
willow	.01
salal	.0143
huckleberry	.01
cedar	.0067
skunk cabbage	.025
sword fern	.025
deer fern	.025
fireweed	.025
arboreal lichens	0.0
douglas fir	.0067
hemlock	.0067

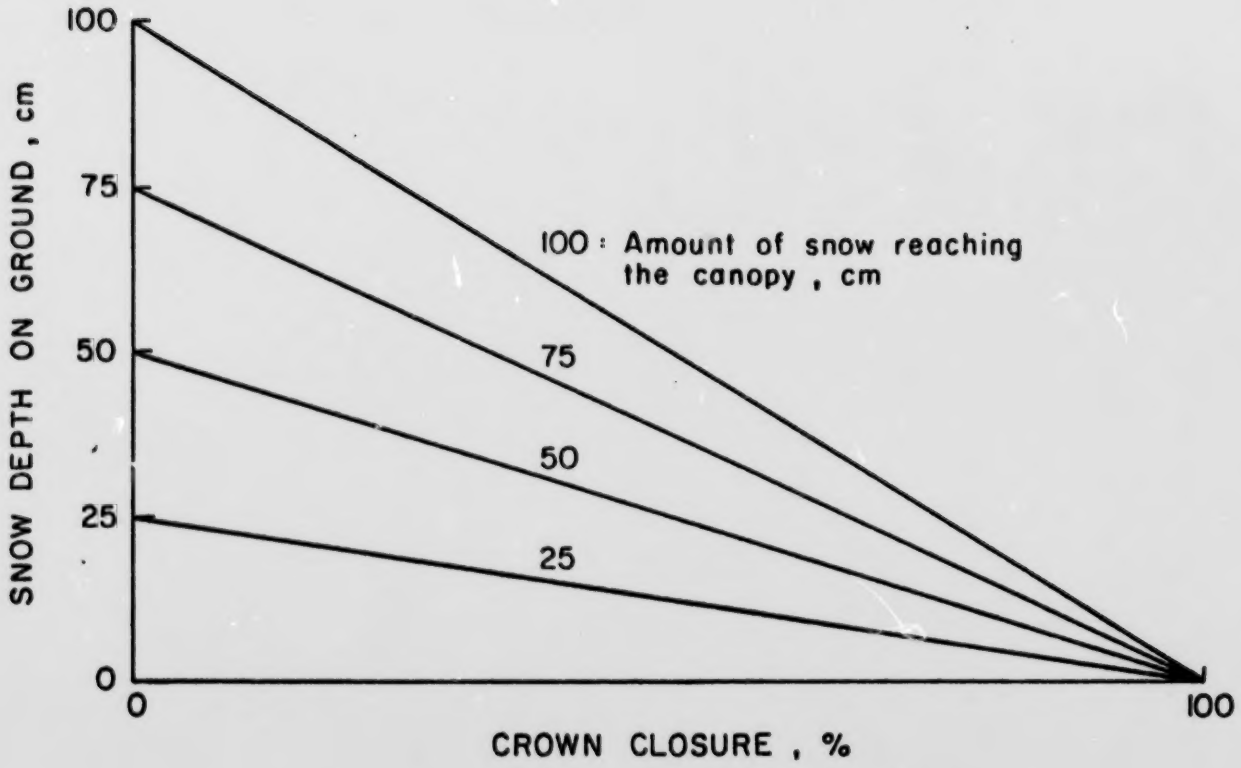


Figure 5.1 Relationship between crown closure and the depth of snow on a site for various levels of snowfall.

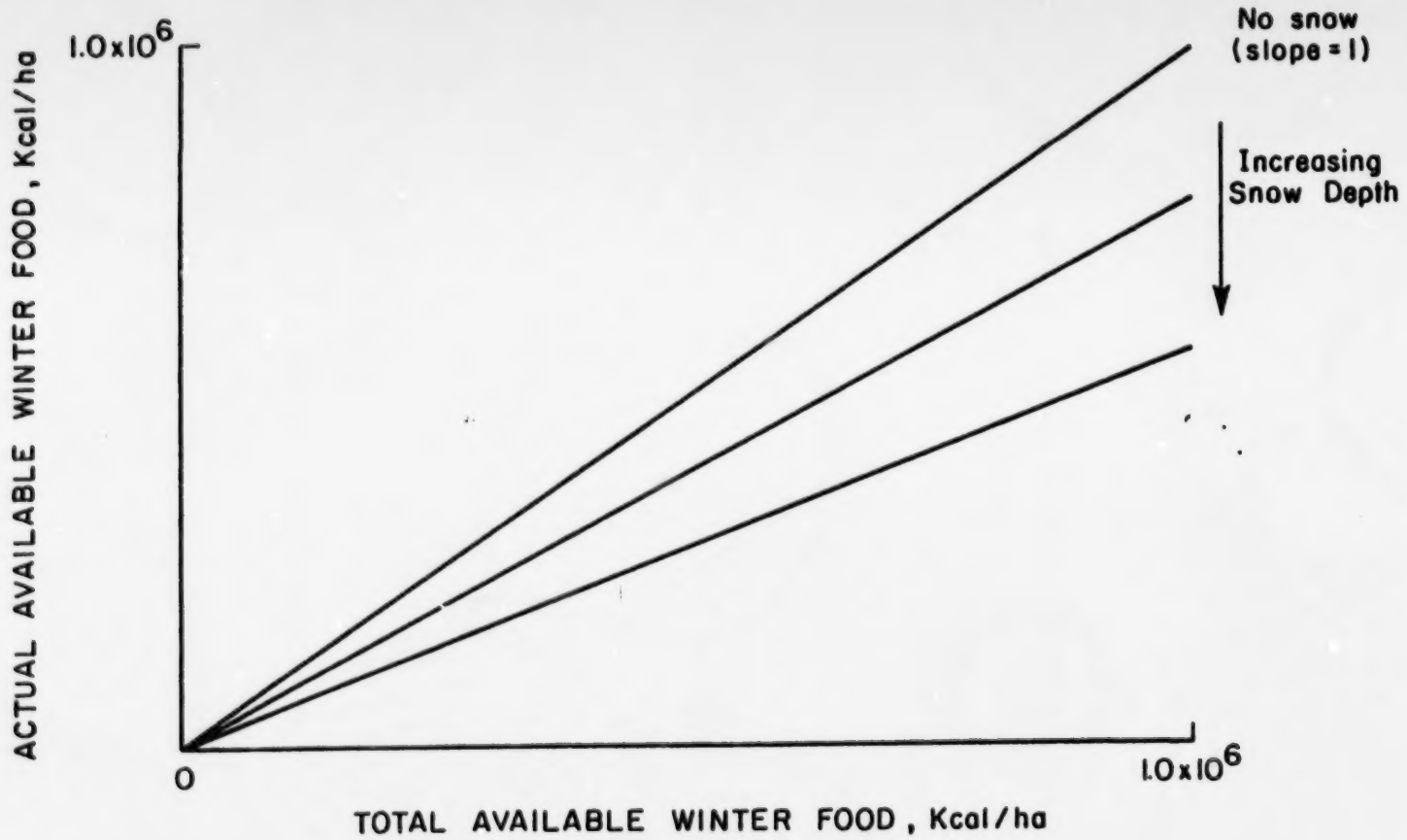


Figure 5.2 The effect of snow depth on the proportion of total food actually not covered by snow.

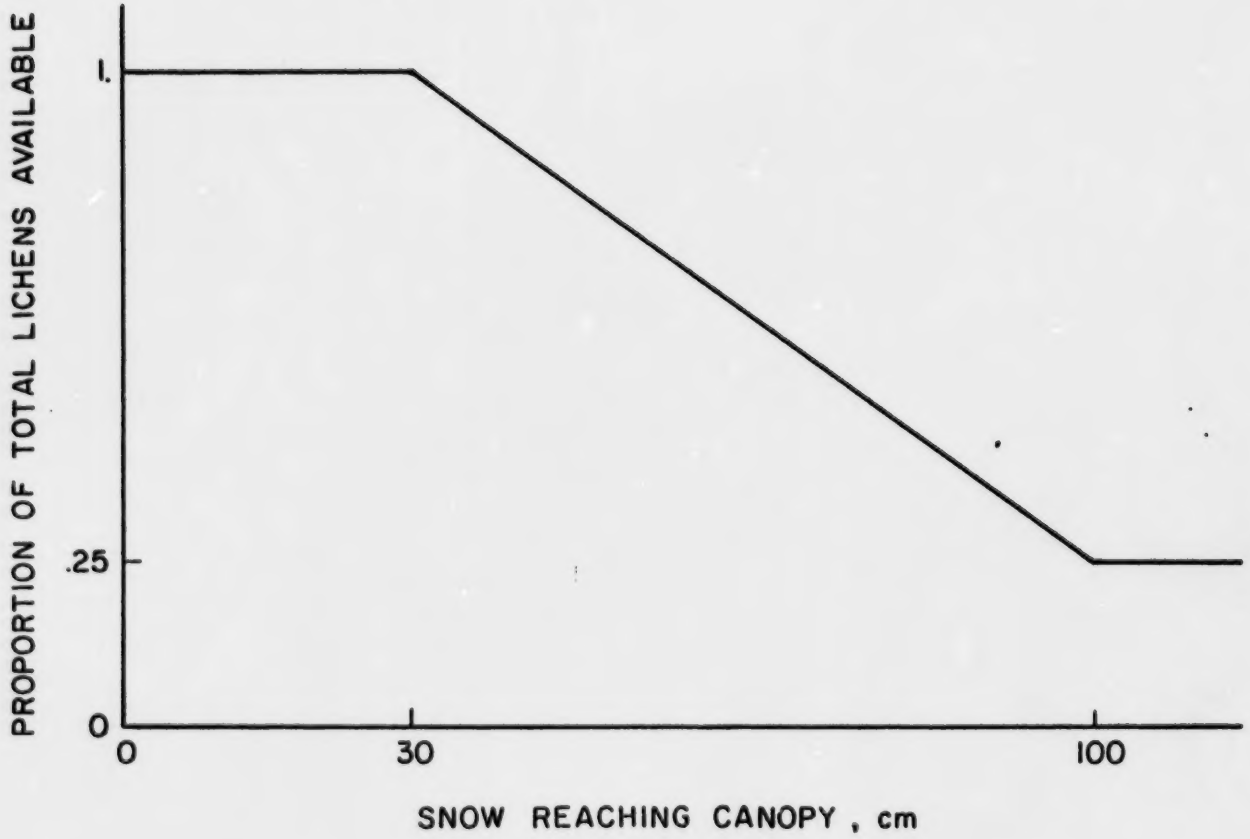


Figure 5.3 Relationship between snowfall and the proportion of total lichens available for feeding.

5.2 Movement

Deer were assumed to modify their distribution among sites at the beginning of each season and to maintain that same distribution throughout the season. Sites were selected on the basis of their relative habitat value according to three criteria: winter range, escape cover and food. Each of these criteria was weighted according to its relative importance. The weighting factors varied with seasonal and subzone (Table 5.2). For example, sites had zero value as winter range habitat in summer. Likewise, winter range in winter was weighted more heavily in the higher subzones.

It was unreasonable to distribute deer to sites based on the value of each site individually because each individual site was considered homogeneous. A site rarely provided a good mix of the three necessary qualities. Habitat for snow protection (i.e., old growth, canopy closed), for example is poor habitat for feeding because of low light penetration. Deer aggregate to groups of sites which collectively provide good habitat. Individual sites were therefore aggregated into blocks of four sites having a common node. No one site was a member of more than one block of four. Thus there were 24 four-site blocks for which the accumulated (over the four sites) habitat value was calculated. The proportion of deer occupying each block was calculated from the following relationship:

$$\text{proportion in block (i)} = \frac{\text{accumulated value of block (i)}}{\sum_{i=1}^{24} \begin{bmatrix}\text{accumulated} \\ \text{value of} \\ \text{block (i)}\end{bmatrix}}$$

Table 5.2 Weighting factors used for determining the relative value of sites as deer habitat. 1 - CDf-Wet; 2 - CWH-Dry; 3 - CWH-Wet.

Season	Subzone	Winter range	Escape cover	Food
	1	0	.2	.8
Spring	2	0	.2	.8
	3	0	.2	.8
	1	0	.5	.5
Summer	2	0	.5	.5
	3	0	.5	.5
	1	0	.5	.5
Winter	2	.4	.2	.4
	3	.5	0	.5

The accumulated habitat value of a block was computed as a weighted sum of its value for winter range, escape cover and forage. The next three subsections describe how the three abovementioned criteria were used to predict the habitat value of a site.

5.2.1 Winter Range

Four components were included in the calculation of a site's value as winter range: crown closure, proportion of total food that was "tall", aspect and lichens. Snow depth directly considered. Since site selection was made at the beginning of a season it was assumed that the deer would distribute themselves on the basis of where they expected snowfall to be a problem rather than were it turned out to be a problem during that particular winter. In essence they had to "decide where to spend the winter" without knowing what the weather would be like that winter.

Figure 5.4a demonstrates the relationship between crown closure on a site and its value as winter range. This value was set equal to zero for all sites with trees less than 2 meters in height (i.e., the site was completely unsuitable as winter range).

Perennials (Section 2.7) were considered to be "tall" food (i.e., more likely to be available when snow is on the ground). The proportion of all available food biomass which fell into the "tall" category was also considered a measure of the value of a site as winter range.

All sites having a northerly aspect were considered only 20% as valuable as winter range as those having a southerly aspect.

Finally, Figure 5.4b describes the relationship between available lichens on a site and its value as winter range. The overall value of a site as winter range was therefore given by the following relationship:

value of site (i) as winter range = crown closure value effect * proportion of food biomass that is "tall"

* .2 [if aspect is north] * [available lichen value effect]

5.2.2 Escape Cover

Two components were considered in evaluating a site's quality as escape cover habitat: tree stem density and tree height (Figures 5.5a, 5.5b). The overall value of the site as escape cover habitat was simply the product of these two components. This value was supplied to the predator submodel, before being modified by its weighting factor, to provide an indicator of the vulnerability of deer to predators on a particular site.

5.2.3 Food

The total digestible biomass of food (summed over all food types) per hectare available in the season under consideration was assumed sufficient to characterize the value of a particular site as feeding habitat (Figure 5.6).

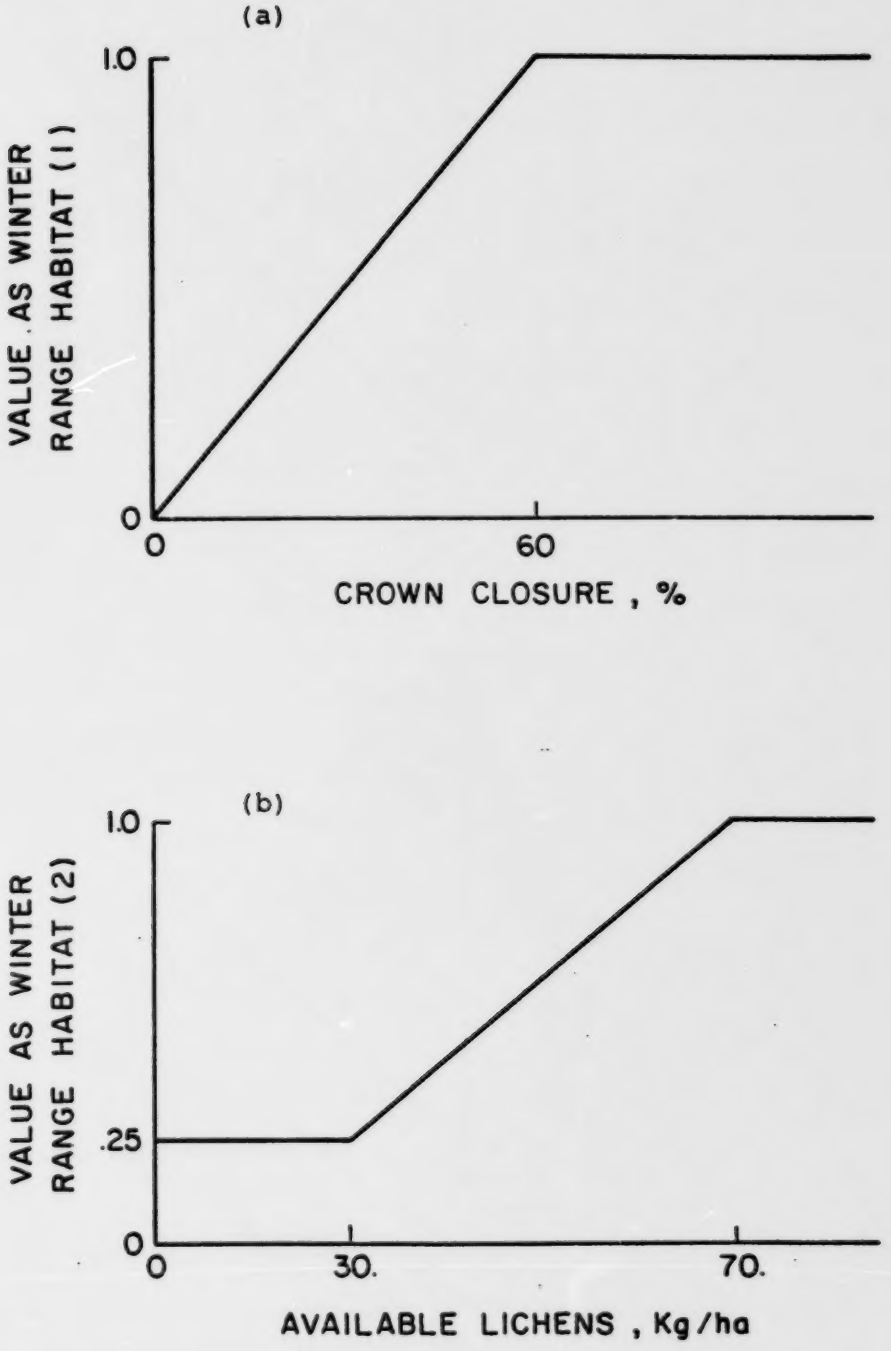


Figure 5.4 Components of the winter range value criterion:
(a) effect of crown closure;
(b) effect of available lichens.

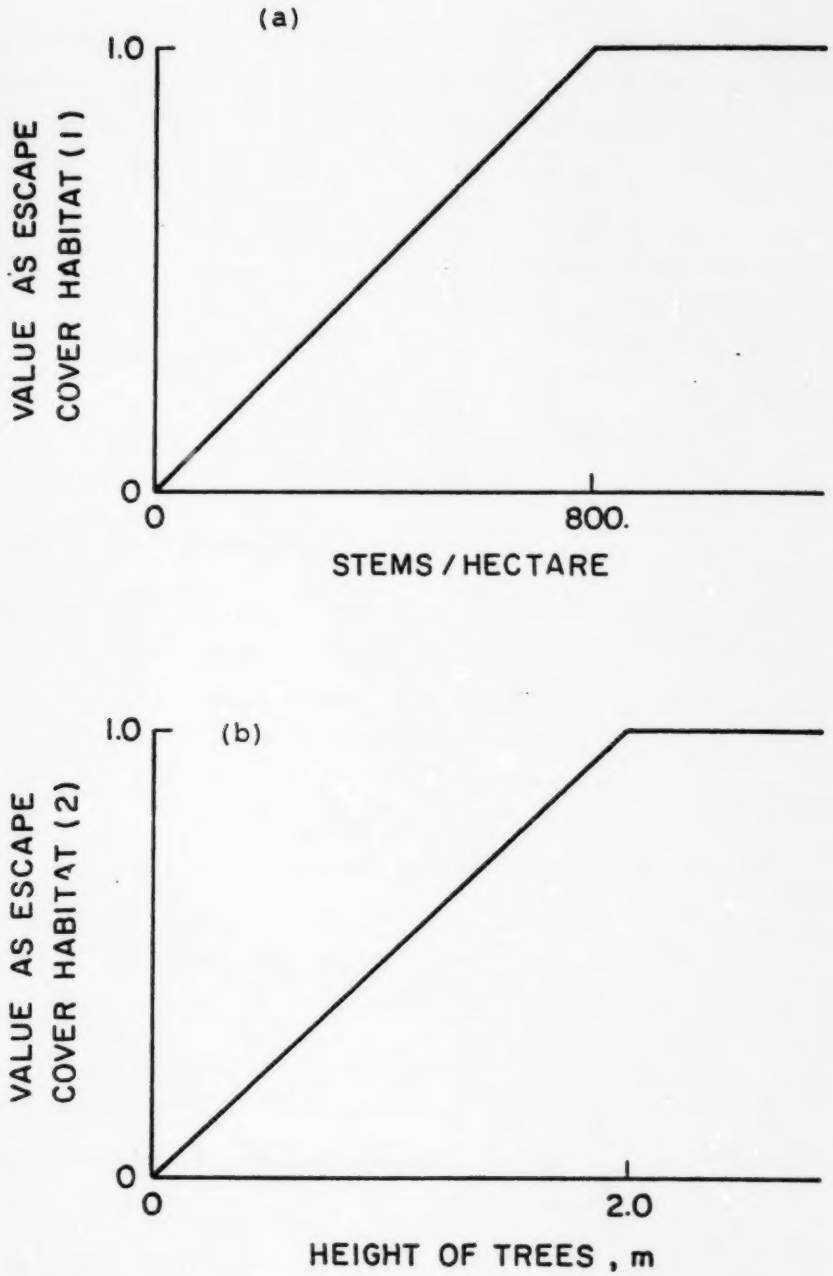


Figure 5.5 Components of the escape cover value criterion:
(a) effect of stem density;
(b) effect of tree height.

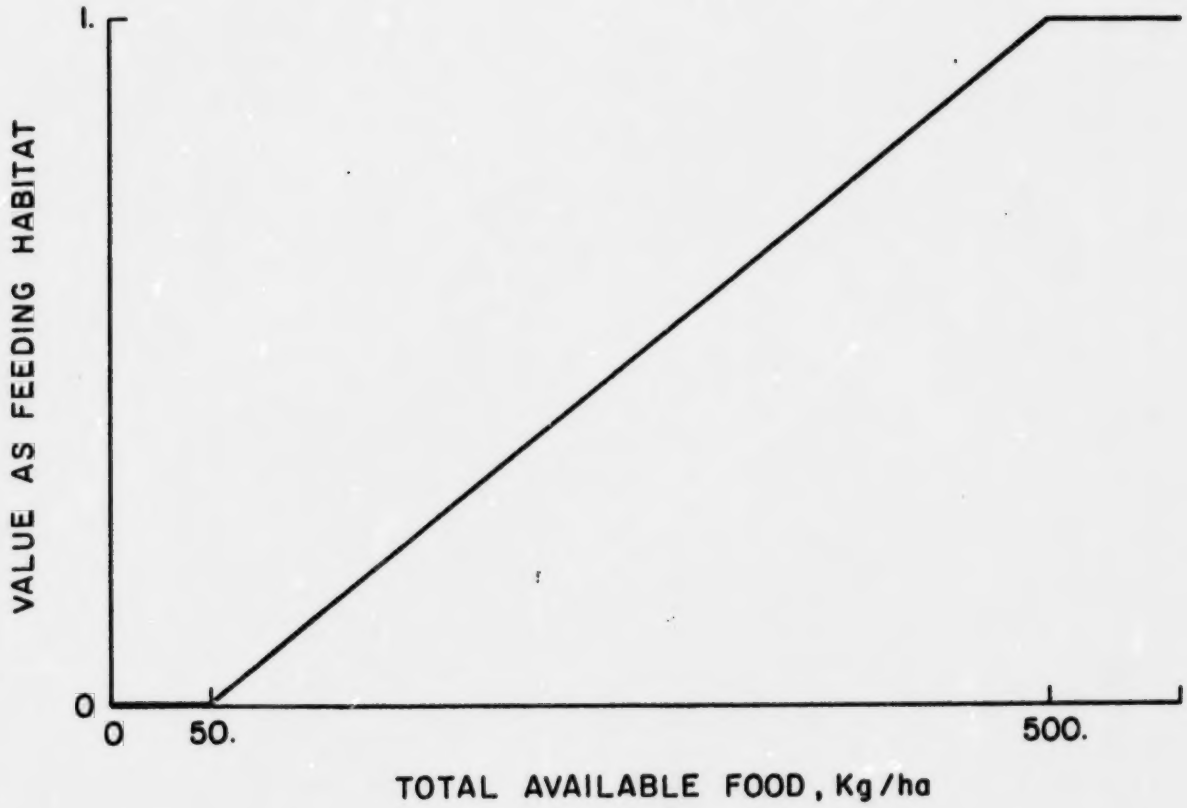


Figure 5.6 The effect of total available food on a site's value as feeding habitat.

5.3 Feeding and Energy Intake

The timber and other vegetation submodels provided the deer submodel with the total biomass available of each food type by site in units of kilograms per hectare. These were converted into season specific quantities representing the kilocalories per hectare of available digestible biomass for each food type on each site (Table 5.3). Next the average over all sites within a single block was computed for each food type. These values were further modified in winter according to the depth of snow on each site in each snowfall period.

Each food type had a season specific preference value and the following relationship was employed (the multi-species disc equation, Charnov 1973) to calcuate the amount of each food type eaten per animal per day on each site:

$$\text{amount(kcal/deer/day) eaten of food type (j) on site (i)} = \text{maximum kcals eaten when food not limiting} \times \text{preference value for food type (j)}$$

$$\times \frac{\text{amount (kcal/ha) of food type (j) available on site (i)}}{\text{searching efficiency parameter} + \sum_{j=1}^{14} \left[\text{preference value for food type (j)}\right] \times \left[\text{amount (kcal/ha) of food type (j) available on site (i)}\right]}$$

The parameters used for this relationship are found in Table 5.4 while Figure 5.7 depicts the form of this relationship for the case where only one food type is preferred.

Table 5.3 Seasonal energy conversion factors from annual forage biomass. These factors are intended to reflect phenological changes in both the availability and caloric value of each food type. Entries in kcal/kg of forage biomass.

Food Type	Season		
	Spring	Summer	Winter
Salmonberry	3230	2500	1400
Elderberry	3534	2000	1800
Willow	3534	2500	1800
Salal	3250	3250	2000
Huckleberry	4297	5120	3150
Cedar	4000	3750	2250
Skunk Cabbage	3800	2500	0
Sword Fern	3380	3750	1880
Deer Fern	3250	4380	1750
Fireweed	4120	6120	0
Other weeds	2280	2500	600
Arboreal lichens	2620	3380	1380
Douglas Fir	4000	4620	2750
Hemlock	3620	5750	2380

Table 5.4 Parameters for the multi-species disc equation used in the calculation of deer food consumption.

Searching efficiency parameter (kcal/ha) 9.0×10^5

	Season		
	Spring	Summer	Winter
Maximum ration (kcal/deer/day)	2600	2400	2000
Preference Indices			
Salmonberry	.1	.1	0.
Elderberry	.08	0.	0.
Willow	0.	0.	.01
Salal	.01	.05	.1
Huckleberry	.08	.25	.2
Cedar	.01	0.	.15
Skunk Cabbage	.01	0.	0.
Sword Fern	.02	0.	.01
Deer Fern	.1	.02	.02
Fireweed	.3	.35	0.
Other weeds	.2	.2	.06
Arboreal lichen	.01	.01	.4
Douglas Fir	.08	.02	.02
Hemlock	0.	0.	.02

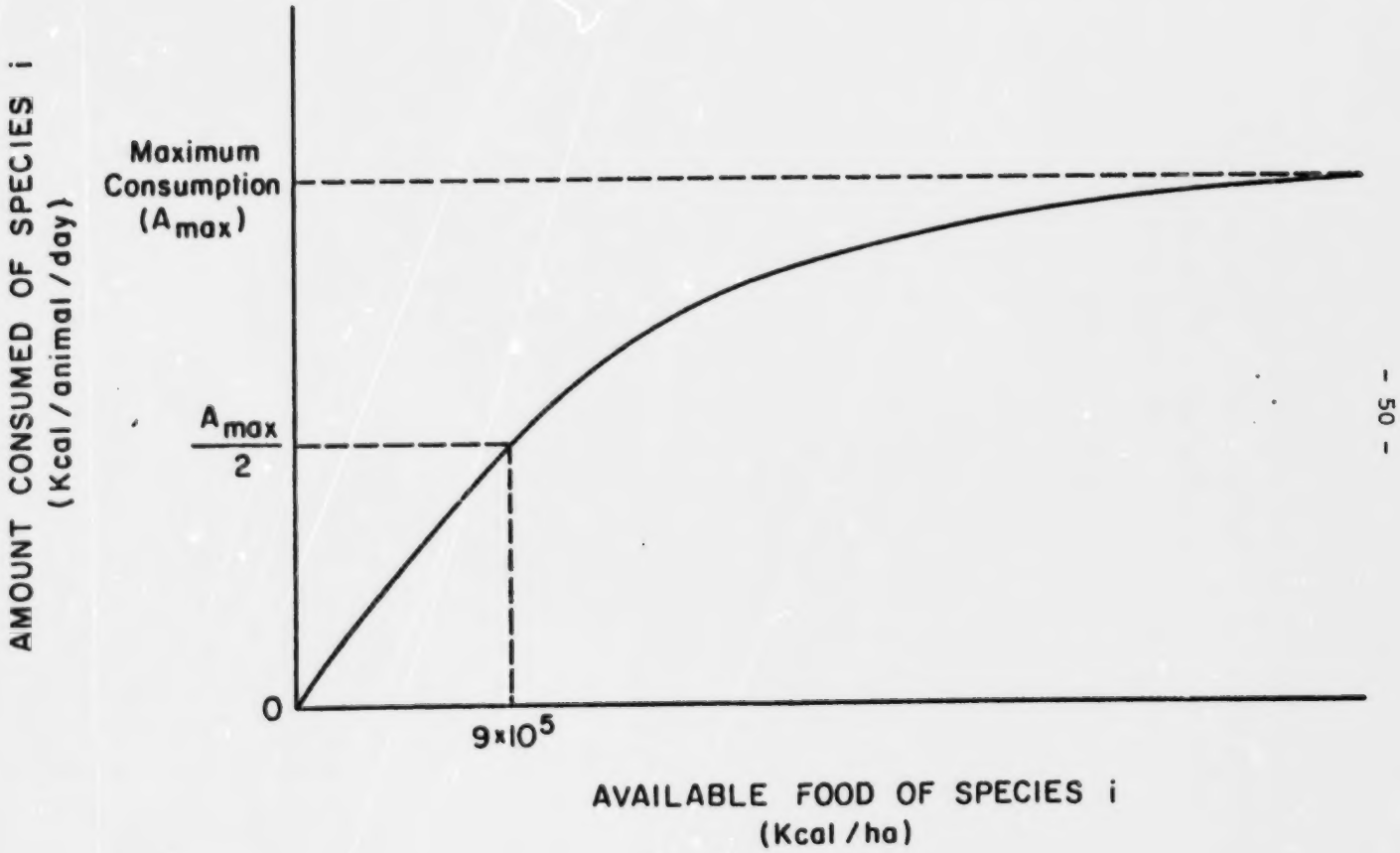


Figure 5.7 The multi-species disc equation: the form of the relationship when only one food type is preferred.

Exploitation was not considered in subgroup discussions but has since been added to the model. Deer are now constrained to eating the available biomass, or their requirements,whichever is lesser. This implies that crowding and interference effects are not important in deer feeding.

Finally, the total annual consumption of each food type on each site was calculated and removed from the available food.

5.4 Survival

All mortality except that resulting from predation was assumed to occur during winter. Baseline age and sex specific winter survival rates (not including predation are given in Table 5.5. The amount of snowfall during winter was hypothesized to influence the energetic costs of deer by hindering locomotion. The energy costs of locomotion were computed for each site for each of the three winter snowfall periods using the following relationship:

$$EL = (SDY)(BMR)(1 + CH \times (SDP \times (1 - SDN/FB))),$$

where EL = locomotory costs for snowfall period (kcal),
SDY = number of days in snowfall period,
BMR = basal metabolic rate (kcal/day),
CH = effect of chest height on locomotory costs,
SDP = snow depth,
SDN = snow density (assumed constant),
FB = snow density above which sinking does not occur.

Energy intake and costs were summed over the three snowfall periods and a "corrected energy balance" computed:

Table 5.5 Parameters used in survival rate calculations.

Age	Sex	Baseline survival rates	Basal metabolic rates (daily)	Winter metabolic requirement (seasonal)	Chest height effect
0-1	F	.75	648 (kcal)	1.1×10^5 (kcal)	.07
	M	.7	599	1.03×10^5	.07
1-2	F	.8	1010.5	1.73×10^5	.062
	M	.8	865	1.48×10^5	.062
2-3	F	.8	1140	1.96×10^5	.06
	M	.8	1201	2.06×10^5	.06
3	F	.7	1140	1.96×10^5	.06
	M	.7	1201	2.06×10^5	.06

snow density threshold = 0.59

$$\text{corrected energy balance for site (i)} = \left[\text{energy intake on site (i)} - \text{locomotary costs on site (i)}\right] \Big/ \text{WMR}$$

where WMR = metabolic requirement over entire winter.

This corrected energy balance value is age and sex specific because animals of different age and sex have different metabolic requirements and chest heights. All parameters of these relationships are provided in Table 5.5.

This corrected energy balance was hypothesized to affect winter survival (Figure 5.8). The weighted (by the proportion of deer on each site) summed over all sites of these age and sex specific values was used to modify the baseline winter survival rates.

5.5 Reproduction

Births were assumed to occur at the start of the summer. Baseline age specific natality rates are given in Table 5.6. These values were assumed to be influenced by energy intake during the previous winter and spring season, with the spring effect being approximately three times as influential as the winter effect. Thus, the age specific corrected energy intake was computed for each site using the following relationship:

$$\text{corrected energy intake for site (i)} = \left[.3 \times \left(\text{winter energy intake}\right) + \text{spring energy intake}\right] \Big/ \left[.3 \times \text{WHR} + \text{SMR}\right]$$

where SMR = metabolic requirements over entire spring (Table 5.6). Figure 5.10 demonstrates the effect of corrected energy intake on natality. A weighted sum over all sites is computed and used to modify the baseline natality rates.

Table 5.6 Parameters used in reproduction calculations.

Age	Baseline natality rates	Spring metabolic requirement (seasonal)
0-1	0.	1.15×10^5 (kcal)
1-2	.91	1.8×10^5
2-3	1.27	2.03×10^5
3	1.69	2.03×10^5

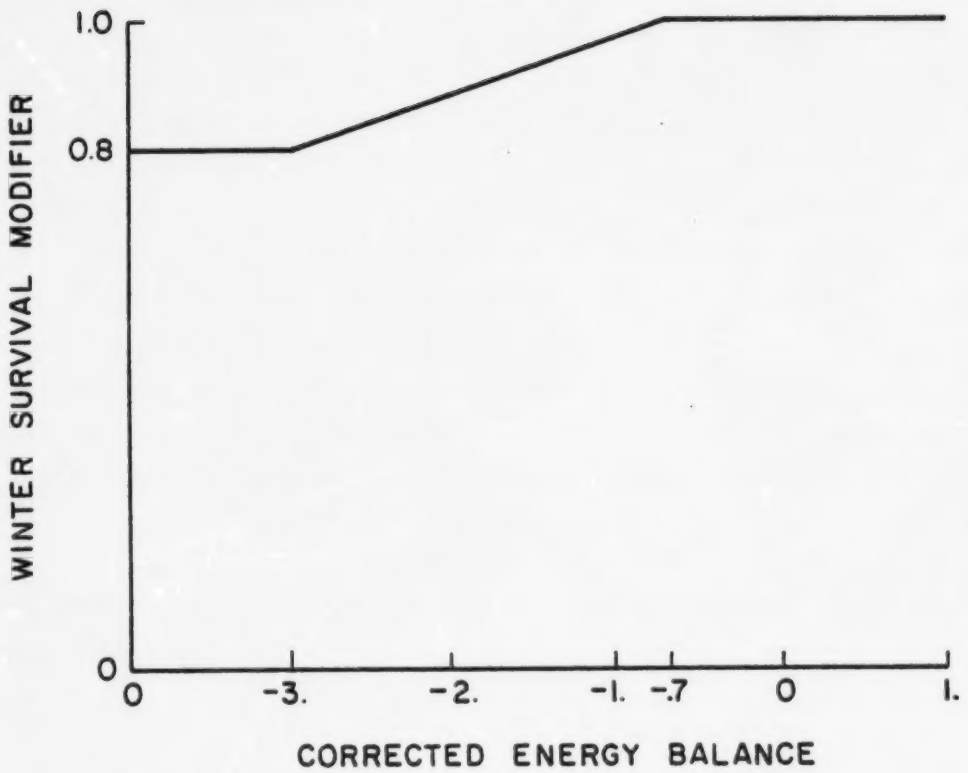


Figure 5.8 The effect of the winter energy balance on winter survival.

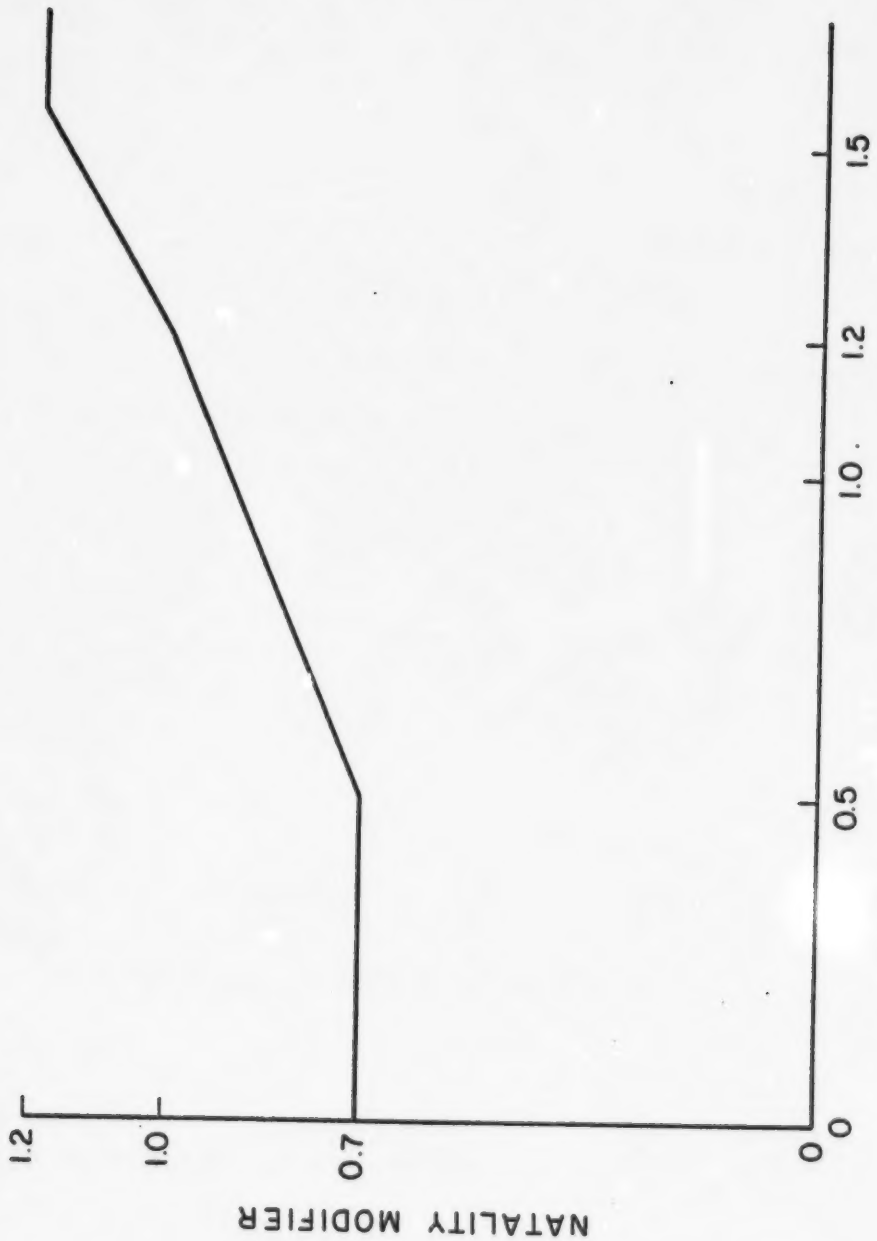


Figure 5.9 The effect of winter and spring energy intake on natality.

6.0 ELK SUBMODEL

The elk subgroup was responsible for developing a conceptual framework that integrated the behavioural and population responses of elk to changing habitat structure and abiotic conditions. Elk were assumed to move throughout the watershed in response to available escape cover, thermal cover, and quantity and quality of forage. Inadequate mixes of available food and cover during various periods of the year and at varying stages of the animal's life cycle were hypothesized to detrimentally affect the potential survivorship and fecundity rates of the population.

The elk submodel was composed of 2 subsections. The first section evaluated the seasonal suitability of each site for elk utilization. This was used to define seasonal movement patterns of elk within the watershed. The second section integrated the quality and quantity of forage over the sites and seasons to generate survivorship and fecundity rate modifiers and used these in a sex and age structured population model.

6.1 Seasonal Site Utilization

The elk subgroup recognized that the movement dynamics of elk are determined by a complex of ecological processes and that the relative importance of the processes varies seasonally. In the spring, elk are found on south aspect slopes, taking advantage of the early new spring growth of specific forage species. During periods of the hot summer, elk likely move to areas with thermal cover on north aspect slopes. Elk are physically excluded during the winter from

areas with very deep snow, while other areas have limited utility because snow depth reduces the quantity of available forage. Elk also continuously aggregate to areas with, or near, adequate predator escape cover.

It was decided to mimic movement dynamics of elk by directly relating the utilization of a site to its relative suitability, and defining site suitability in terms of those ecological attributes important in determining population responses.

Suitability was hypothesized to be a function of the seasonal digestible energy in the forage, modified by site and season specific physical constraints, and the availability of escape cover:

$$\text{suitability}_{ij} = \begin{pmatrix}\text{digestible}\\ \text{energy of}\\ \text{forage}\end{pmatrix}_{ij} \begin{pmatrix}\text{physical}\\ \text{constraint}\\ \text{modifiers}\end{pmatrix}_{ij} \begin{pmatrix}\text{escape}\\ \text{cover}\\ \text{value}\end{pmatrix}_{i}$$

where i is the site and j is the season. Escape cover is evaluated only once annually. Both modifiers were scaled between 0 and 1. The level of utilization of a site was therefore given by:

$$\text{suitability}_{ij} / \sum_{i=0}^{96} \text{suitability}_{ij}$$

6.1.1 Seasonal Digestible Energy

The contribution from each potential forage species to the seasonal disgestible energy available to elk on a site was the product of the available annual biomass of the species in the site, the kilocalories of digestible food energy per kilogram for that species for a given season,

and a seasonal species preference factor that ranged between 0 and 1. Available annual biomass had to be modified seasonally to adjust for within-year changes in plant availability (Section 5.3). For example, an herbaceous annual may have zero kilocalories of food energy in the winter simply because it is no longer available. The species preference factor simulates the apparent preferences shown by elk for particular species and the seasonal variability of those preferences. A site with a moderate biomass of a highly preferred browse species would have a higher value than a site with a large biomass of relatively unpreferred browse and elk would spend more time and consume more forage in the preferred site. The seasonal forage preference values are listed in Table 6.1.

The seasonal digestible energy for a site was calculated by simply summing the individual digestible energy over all species each season.

6.1.2 Escape Cover

Adequate elk escape cover was defined as any site within critical minimum and maximum stand densities of trees greater than a minimum critical height (Figure 6.1). Any site within these constraints was assigned an escape cover value of 1. The upper stand density was never realized on the managed stands.

Sites with inadequate escape cover but adjacent to sites with good escape cover were assumed to be partially utilizable. For example, elk could forage in a portion of a clear cut as long as adequate escape cover was nearby. The escape cover value of a site with inadequate cover was related to the nearness of that site to the nearby site with maximum cover value. Therefore, a

Table 6.1 Seasonal food preferences for elk.

Species	Spring	Summer-Fall	Winter
Salmonberry	.6	1.	0.
Elderberry	.3	.5	1.
Willow	.4	.5	1.
Salal	0.	0.	.4
Huckleberry	.1	.3	.4
Cedar	0.	0.	.5
Skunk Cabbage	1.	.8	0.
Sword Fern	.4	0.	.2
Deer Fern	0.	0.	.6
Fireweed	.1	.1	0.
Other Weeds	1.	1.	.5
Douglas Fir	0.	0.	.2
Western Hemlock	0.	0.	.1
Arboreal Lichen	0.	0.	.4

Table 6.2 Temporal utilization rates for elk. The utilization rates represent the proportion of times that the stands are usable by elk.

SPRING

Moisture Regime	Subzone:	1		2		3	
	Aspect:	North	South	North	South	North	South
1		.2	.2	.2	.2	.2	.2
2		.2	.2	.2	.2	.2	.2
3		.6	.2	.6	.2	.4	.2
4		.6	.6	1.0	.7	1.0	.7

WINTER

Moisture Regime	Subzone:	1		2		3	
	Aspect:	North	South	North	South	North	South
1		.2	.2	.2	.2	.2	.2
2		.3	.2	.4	.2	.2	.2
3		.4	.3	.8	.4	.5	.2
4		.8	.45	.8	.2	.2	.2

SUMMER-FALL

Moisture Regime	Subzone:	1		2		3	
	Aspect:	North	South	North	South	North	South
1		.2	.2	.2	.2	.2	.2
2		.2	.2	.2	.2	.2	.2
3		.2	.2	.2	.45	.4	.5
4		.2	.4	.4	.9	.45	1.0

site with adequate escape cover conferred an escape cover value of 0.5 to neighbouring sites with inadequate cover that shared a common side, and an escape cover value of 0.25 to neighbouring sites with inadequate cover that shared only a common corner (Figure 6.2). The "edge effect" or the effect of clear cut size could be explored by changing the magnitude of the influence of sites with adequate cover on adjacent sites. Elk were assumed to not use sites with an escape cover value of 0.0. As a result, the term "adequate cover" does not mean that the elk are invulnerable to predation or will not suffer thermal stress, but rather, elk will not be found in areas with "inadequate" access to cover.

6.1.3 Physical Constraints

Physical constraints were hypothesized to affect the suitability of a site to elk. The elk subgroup used site subzone, moisture type and aspect as indicators of physical site suitability and seasonally modified the relative importance of each to reflect changes in preferences of elk for different physical locations throughout the year.

The effects of snow on site suitability were considered. The winter was divided into three periods of variable duration that represented three depths of snowfall (Section 5.1). These different depths of snow were also assumed to alter the availability of the understory forage (Section 5.1.3). The elk subgroup also assumed sites with snow over 1.2m average depth on the ground were unavailable to elk.

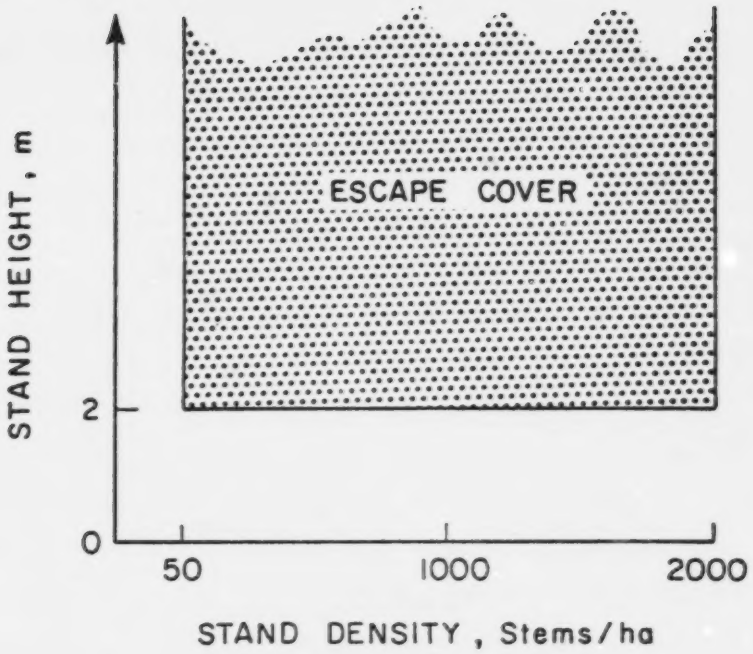


Figure 6.1 Elk escape cover as defined by stand height and stand density

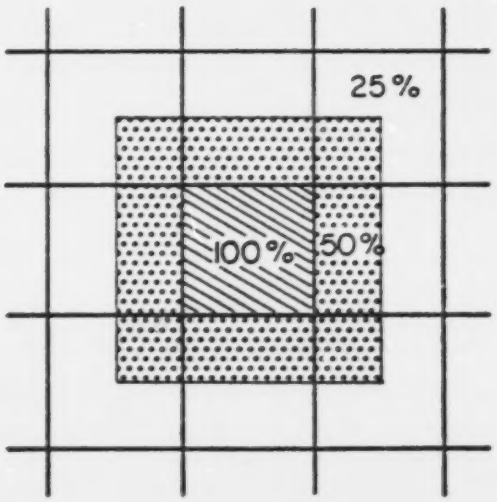


Figure 6.2 Extension of utilization potential from a cell with complete cover to neighbouring cells with no cover.

6.1.4 Calculation of Seasonal Site Utilization

The suitability of a site for elk use was calculated as the product of its seasonal digestible energy, escape cover value, scaled between 0 and 1, and seasonal physical suitability, also scaled between 0 and 1. The product represented that site's available caloric food value for elk. The relative caloric food value represented the level of utilization of that site by elk, or the proportion of a season the elk population would spend feeding in that site.

6.2 Population Dynamics

The population dynamics of elk were simulated using an age class population model with four age classes - fawns, yearlings,. two year olds, and adults, for each sex. The maximum assumed survivorship rates are listed in Table 6.3. The maximum assumed fecundity rates were .8 and .95 per 2 year old and adult elk respectively. These rates could all be reduced if there was insufficient caloric forage value (Section 6.1.4) in the watershed to meet the caloric requirements of the population.

6.2.1 Seasonal Energy Requirements

The seasonal energy requirements for the elk population were determined by the product of the number of elk in each age and sex class and the average seasonal caloric requirements specific to each age and sex class (Table 6.4). The metabolic rates incorporate differences in weights, lactation costs, rutting costs and growth costs. In winter,

elk were assumed to suffer an extra locomotion cost in the presence of snow for those sites with a snow depth less than 1.2m (Figure 6.3). The elk population's winter metabolic rate was thus modified by the depth of snow in each site and the proportion of time the population spent in each site.

6.2.2 Survivorship

The elk subgroup assumed that the potential survivorship rates for each age and sex class would be reduced by inadequate available energy. The reduction in survival was assumed to depend on both the severity and duration of the shortage.

These effects were simulated by calculating an average daily mortality rate for each age and sex class as a function of the ratio of available calories in the watershed to the caloric requirements of the elk population (Figure 6.4). In the model, the function is characterized by two parameters: the maximum daily mortality rate and that ratio of available calories to required calories (or density of food per elk) at which the mortality rate would be reduced to half of its maximum value (Table 6.5).

Average daily mortality rates were converted to seasonal or "snow period" mortality rates and were combined over all seasons and periods to give yearly survivorship rate modifier for each age and sex class.

Table 6.3 Potential survivorship rates for elk.

	Male	Female
calf	.80	.80
yearling	.85	.9
two year old	.94	.94
adult	.75	.9

Table 6.4 Average daily caloric requirements (kcal/day) for elk by sex, age class and season.

	Spring		Summer		Winter	
Class	M	F	M	F	M	F
calf	4180	3540	4180	3540	3396	2877
yearling	6550	5960	6550	5960	5324	4840
two year old	7040	7257	7040	7257	5720	5540
adult	8070	8325	8070	8325	6560	6365

Table 6.5 Maximum average daily mortality rate due to starvation and the ratio of available forage (calories) to population forage requirements (calories) required to reduce the mortality by 50%.

	Max. mortality rate all sex/age classes	Ratio for half mortality							
		Male				Female			
		fawn	1yr.	2yr.	adult	fawn	1yr.	2yr.	adult
Spring	.00274	1	1	1	1	1	1	1	1
Summer	.00274	1	1	1	1	1	1	1	1
Winter	.00274	1	.4	.4	1	.6	.6	.6	.6

Table 6.6 Maximum average daily reduction in fecundity due to starvation and the ratio of available forage (calories) to population forage requirements required to reduce the reduction rate by 50%.

	Max. daily fecundity reduction	Ratio for half of the reductions		
		Spring	Summer	Winter
two year olds	.00274	1	1	1
adult	.00274	1	1	.8

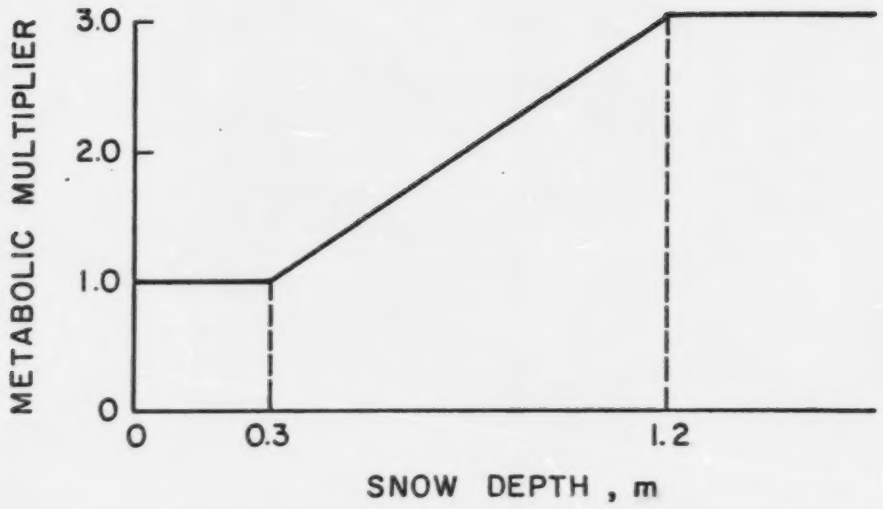


Figure 6.3 Energetic cost of moving in snow for elk as a multiple of the elk's basic metabolic rate.

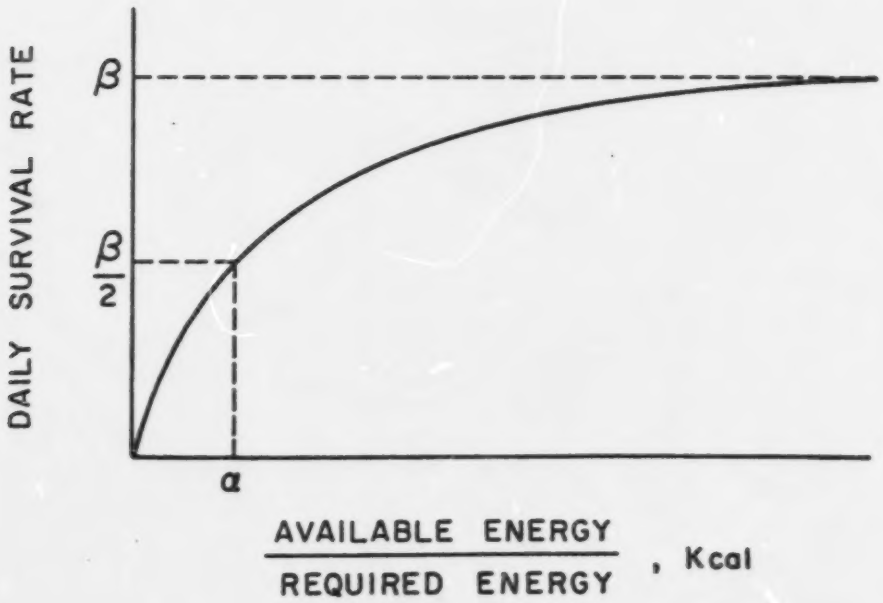


Figure 6.4 Effect of food availability on elk survival. β and α are age-class and sex specific and are summarized in Table 6.5. The functional form of fecundity reduction is the same.

6.2.3 Fecundity

The two year old and adult female fecundity rates were also modified using the ratio of available calories to required calories. As in the survivorship modifier the functional relationship needed two parameters: the maximum average daily percent reduction in fecundity as a result of food shortages and that ratio of available calories to required calories at which the average daily reduction in the fecundity rate would be half of its maximum value (Table 6.6). These average daily reductions in the fecundity rates were multiplied by the number of days in the season or snow period to generate seasonal reductions in the fecundity rates and combined to reduce the maximum annual fecundity rates for the apropriate sex and age classes.

Forage was removed from each site in proportion to the total caloric requirements of elk, the availability of each browse species, and the site utilization.

6.2.4 Population Change

Elk were aged annually using the natural survivorship rates and the survivorship modifiers (Section 6.2.2) and calves were produced using the maximum fecundity rates and the fecundity modifiers (Section 6.2.3). The sex ratio of calves was assumed to be constant at 50%.

The elk subgroup assumed that elk would emigrate from the watershed if the total elk population exceeded 60 animals. The sex ratio for the emigrants would be 70% males.

7.0 PREDATION AND HUNTING

The predation and hunting subgroup was responsible for developing a conceptual framework for predicting the effects of predators and hunters on deer and elk populations, given age and sex specific densities of deer and elk and escape cover.

The subgroup considered predation by wolves, cougars, and bear.

7.1 Distribution of Predation

Predators were hypothesized to respond differently to densities of young of the year and all other prey. Predator kills were apportioned to each sex and/or age group within those two population classes according to the relative abundance of each group.

Predation rates were calculated annually and apportioned seasonally according to Table 7.1.

7.2 The General Model

Predation was simulated using classical predator-prey theory, with functional and numerical responses (Solomon, 1949). The model explicitly considers changes in the number of kills per predator in response to changes in prey density (functional response) and changes in the number of predators in response to changes in prey density (numerical response).

Table 7.1 Seasonal distribution of predation. Proportions indicate the amount of the yearly predation that is assumed to occur in each season.

		Fawn/Calf			Adult		
		Spring	Summer-Fall	Winter	Spring	Summer-Fall	Winter
Deer:	wolf	.1	.6	.3	.2	.3	.5
	cougar	.2	.3	.5	.2	.3	.5
	bear	0.0	1.0	0.0	0.0	0.0	0.0
Elk:	wolf	.2	.3	.5	.2	.3	.5
	cougar	.1	.7	.2	.1	.7	.2
	bear	0.0	0.0	0.0	0.0	0.0	0.0

Predation is one of the most-studied and best understood ecological process. The use of well-understood models ensured that the biological interpretation of the uncertainties in modelling predation on elk and deer could be easily translated into well-defined research questions. The types of functional and numerical responses used in the model are summarized in Tables 7.2 and 7.3.

Interaction between predators was assumed not to occur.

7.3 Influence of Escape Cover

Escape cover for deer and elk was assumed to affect their vulnerability to predation by reducing the number of prey available to predators. A vulnerability factor based on the proportion of the region classified as good escape cover was calculated (Figure 7.1). Every animal is vulnerable to predation with no escape cover and only 50% of the total population is vulnerable to predation with maximum escape cover.

7.4 Wolf Predation

Wolf packs on Vancouver Island are small and wolves have been seen hunting singly or in pairs. Because of the small pack size, wolf functional responses were defined in terms of kills per wolf rather than than kills per pack.

Table 7.2 Functional responses of predator to prey.

	Deer	Elk
Wolves	density dependent	density dependent when deer density is low
Bear	density dependent	density dependent
Cougar	density dependent	density dependent

Table 7.3 Numerical response of predators to prey.

	Deer	Elk
Wolves	density dependent	density independent
Bear	density dependent	density independent
Cougar	density dependent	density independent

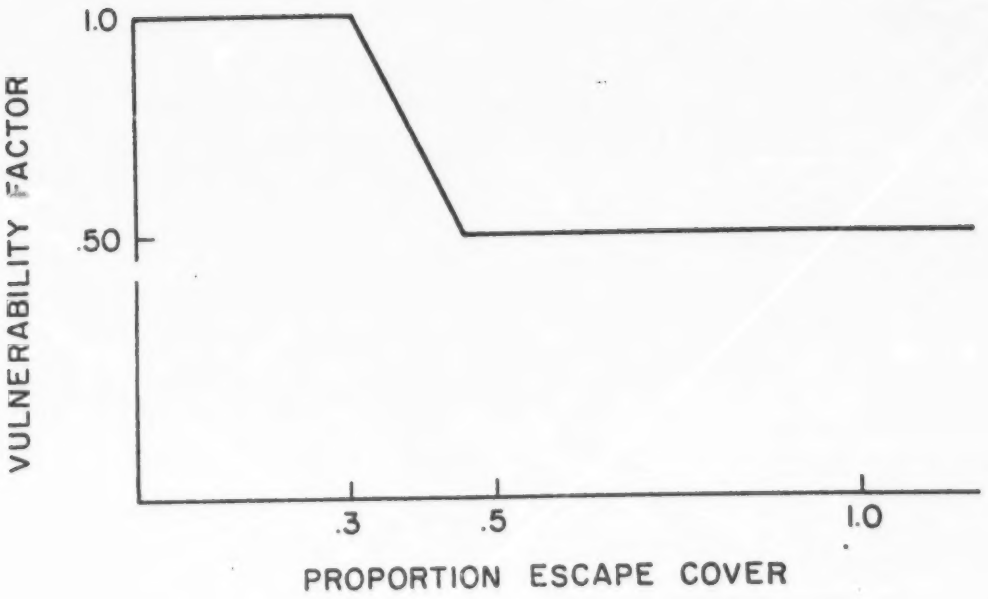


Figure 7.1 Vulnerability factor for deer based on escape cover.

7.4.1 Deer-Wolf Interactions

7.4.1.1 Functional Response

A major underlying assumption in the model is that deer and wolf form a tightly coupled predator-prey system. It was therefore hypothesized that there is a range of deer densities within which the yearly food requirements of an adult wolf (about 820 kg) are almost solely satisfied by deer. Because of this assumption the wolf functional response to fawns (Figure 7.2a) and wolf functional response to adults (Figure 7.2b) had to be developed simultaneously. In developing the functional responses, fawns were assumed to weight 9 kg and adults 54kg. The functional response to adults (Figure 7.2) depends critically on the fawn-adult ratio. More adults are taken by predators as the fawn-adult ratio decreases. The hypothesized relationship between fawns killed per wolf per year and the fawn density (Figure 7.2) is S-shaped. The assumptions in this response form are:

(a) wolves prey on alternate sources of prey at low densities of deer;

(b) there exists a threshold density at which deer become almost the sole source of food for wolves; and

(c) there exists another threshold density at which ratio of fawn to adult biomass in the wolf's diet becomes constant.

The threshold densities depend on the fawn-adult ratio. Figures 7.2a and 7.2b show the two functional responses for a fawn-adult ratio of 1.0.

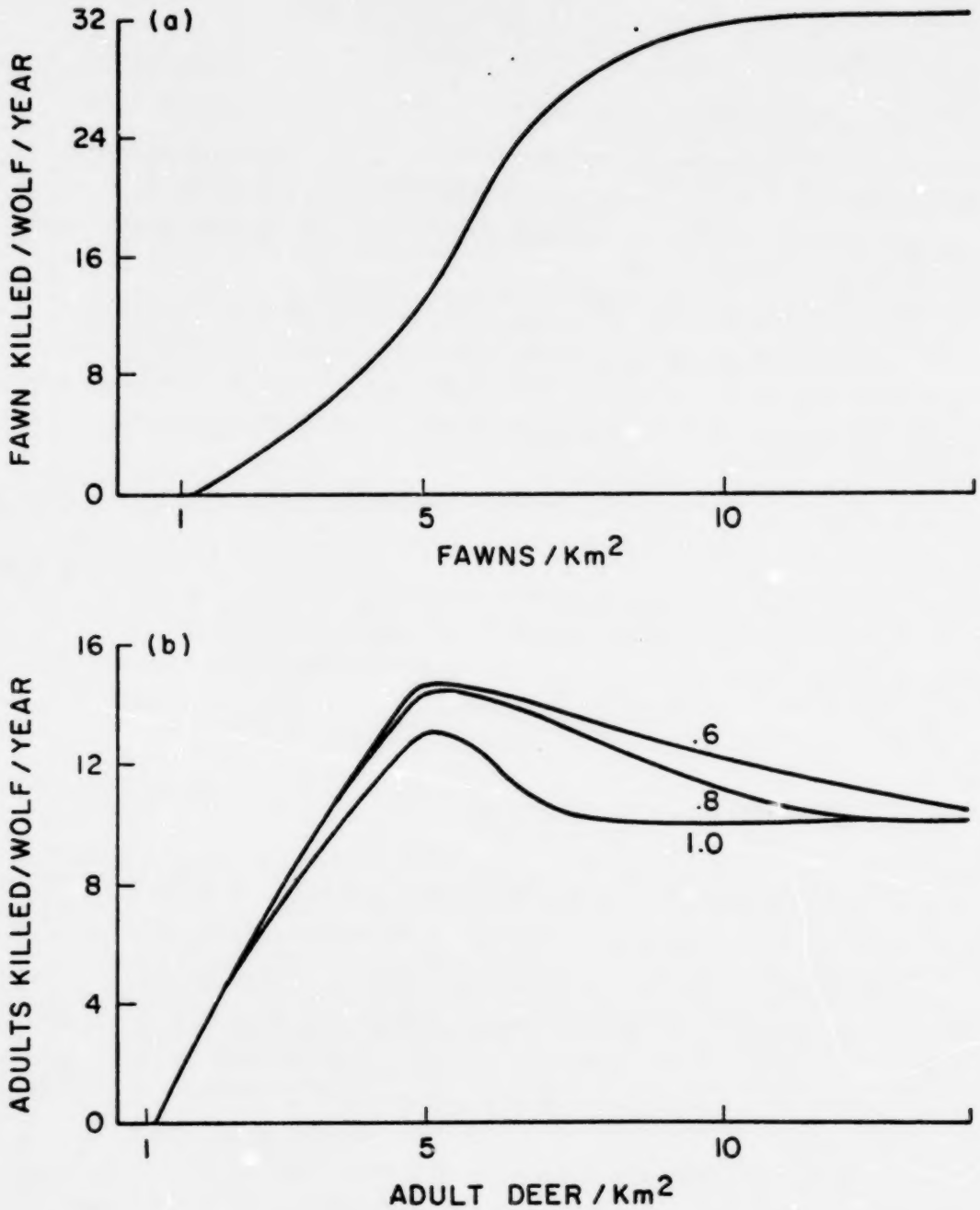


Figure 7.2 Functional responses of wolves to fawn density (a) and adult deer density (b).

7.4.1.2 Numerical Responses

It was hypothesized that wolf abundance would not change in the deer density range within which their food requirements are primarily satisfied by deer and the fawn-adult ratio in wolf kills increases with increasing density (Figure 7.2). The concept of deer adult equivalents is simply that six fawns are equivalent in biomass to one adult deer. It was assumed that wolves show a positive numerical response due to increased pup survival and immigration when deer densities become greater than 12 deer adult equivalents/km^2 and a negative numerical response due to decreased pup survival, starvation, and emigration at densities less than 6 deer adult equivalents/km^2. Wolves are assumed to shift to alternate prey sources at deer densities less than 6 adult equivalents/km^2 but not be able to make up for the decrease in food from deer predation (Figure 7.3).

7.4.2 Elk-Wolf Interactions

Wolves were hypothesized to prey primarily on elk calves. The form of the functional response of wolves to elk (Figure 7.4) assumes that the number taken is constant as long as deer are the primary food source for wolves (i.e., deer densities greater than 6 adult equivalents/km^2). Wolves show a linear functional response to elk density, measured in elk adult equivalents, for deer densities less than 6 adult equivalents/km^2 (4 elk calves are approximately equal to one elk adult).

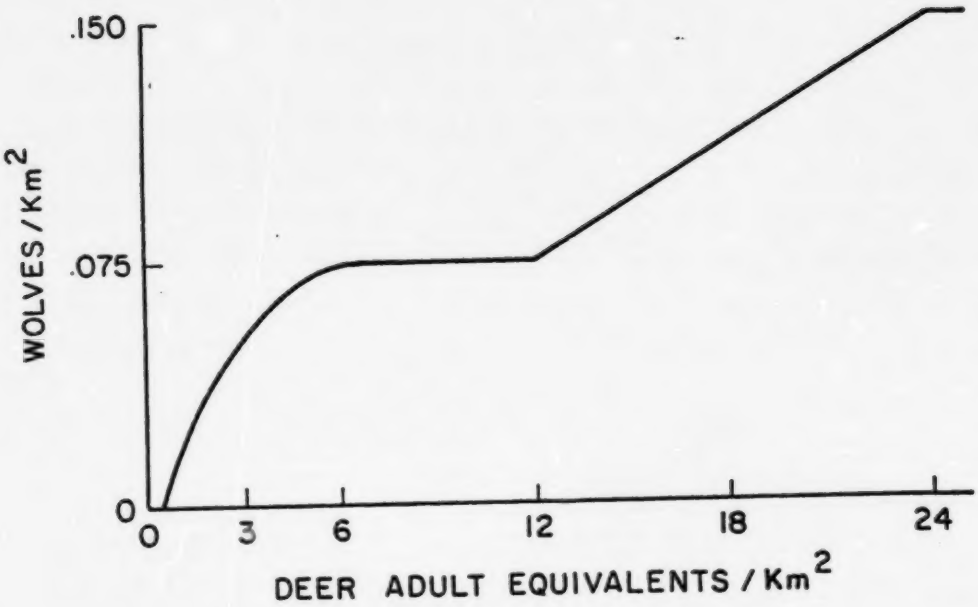


Figure 7.3 Numerical response of wolves to deer density.

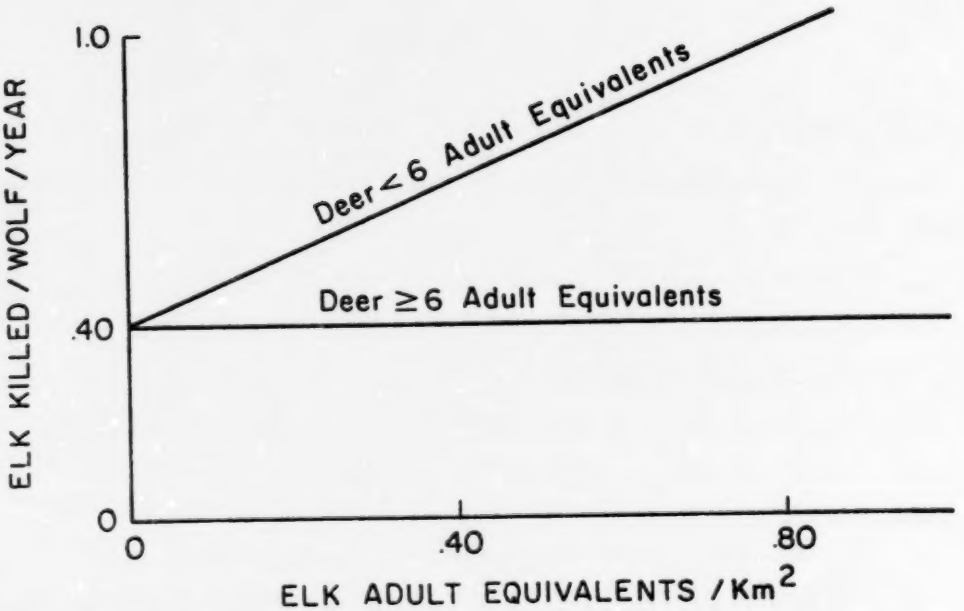


Figure 7.4 Functional response of wolves to elk density.

7.5 Bear Predation

Bears prey only on fawns and only in the summer in the model. Bears are hypothesized to have no numerical response to prey density; a constant 6 bears in the watershed is assumed. The bear functional response to fawn density (Figure 7.5) is linear up to 9 kills per bear per year at 10 fawns/km^2 and constant at 9 kills with greater prey densities.

7.6 Cougar Predation

Cougars are hypothesized to show no numerical response to either deer or elk.

7.6.1 Deer-Cougar Interactions

The model assumes a constant 2 cougar and 2 kittens and treats them as 3 cougar adult equivalents. The cougar functional response to deer density (Figure 7.6) is assumed linear up to a threshold of 50 deer kills per cougar per year at 10 deer/km^2 and constant at 50 kills with greater prey densities. The fawn-adult kill ratio is assumed to be 4:1.

7.6.2 Elk-Cougar Interactions

Cougars are assumed to have a density-independent functional response to elk. This implies they have no handling time when preying on elk. The model currently assumes each cougar kills 1.6 calves and 0.4 adults per year.

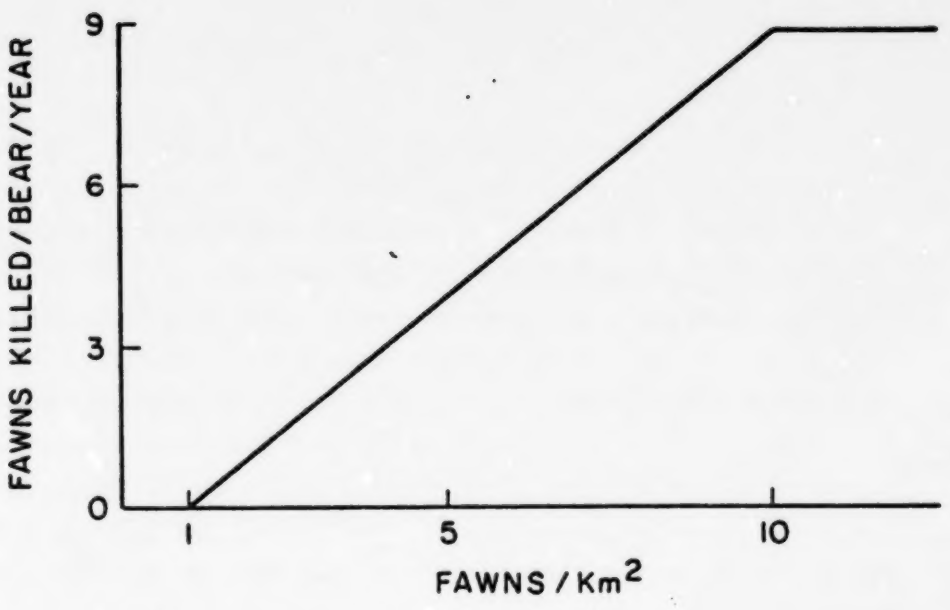


Figure 7.5 Functional response of bear to fawn density.

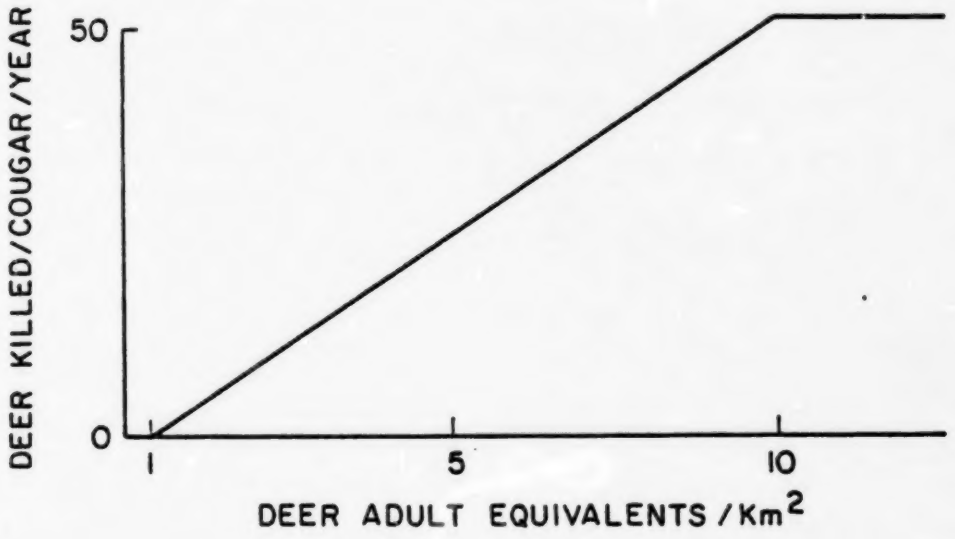


Figure 7.6 Functional response of cougar to deer density.

7.7 Hunting

The model does not explicitly consider the dynamics of hunting, but the harvest rate function implicitly includes increases or decreases in hunting effort in response to deer density (Figure 7.7). The decline in the harvest rate as deer populations increase from low densities is based on the assumption that there is a group of hunters who always kill the same number of deer over a range of low deer densities. Less efficient hunters become more successful at higher deer densities until a maximum harvest rate is reached. The total number of deer taken by hunters is allocated by age and sex using the following proportions:

	fawn	yearlings	adult (2+)
Male	.05	.50	.25
Female	.05	.075	.075

The elk hunt was not modelled as it was not believed to be significant because of the current permit system for licensing elk hunters.

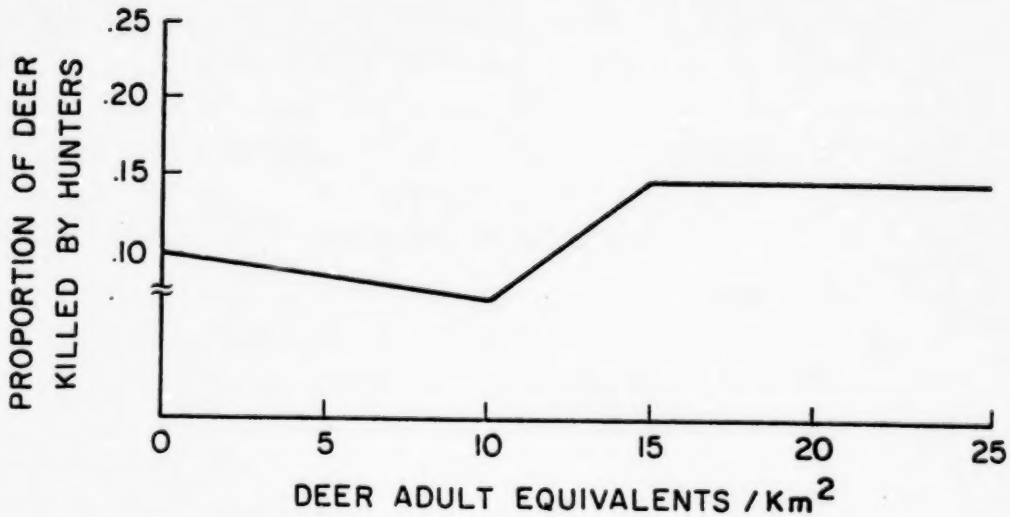


Figure 7.7 Hunter harvest rates as a function of deer density.

8.0 RESULTS OF THE WORKSHOP

8.1 The Conceptual Model

Once the submodels were constructed they were linked together using the information transfers identified in the looking outward exercise (Section 2.6). The complete model is a complex of numerous relationships within and between submodels but a compression and simplification of the complete model (Figure 8.1) gives a broad understanding of the causal relationships between components of the model. Many of the processes outlined in the conceptual model are influenced by the physical characteristics of the region such as subzone, moisture type, and aspect and many of the processes, such as snowfall and food preferences, vary seasonally.

Not all links defined in the looking outward exercise were included in the model built at the workshop. These omissions have been noted in the previous submodel descriptions and will be discussed in Sections 8.2, 8.4, and 9.

8.2 Conceptual and Information Needs

The actual process of building a model of a biological system always reveals deficiencies in conceptualization and understanding of system processes and dynamics. In the context of the objectives of the workshop, identification of these deficiencies is critically important in developing a research plan for IWIFR. This section will be devoted to a formal identification of these conceptual and information needs. Since most of these needs were uncovered during the subgroup discussions they will be categorized according to the submodel with which they are most closely associated.

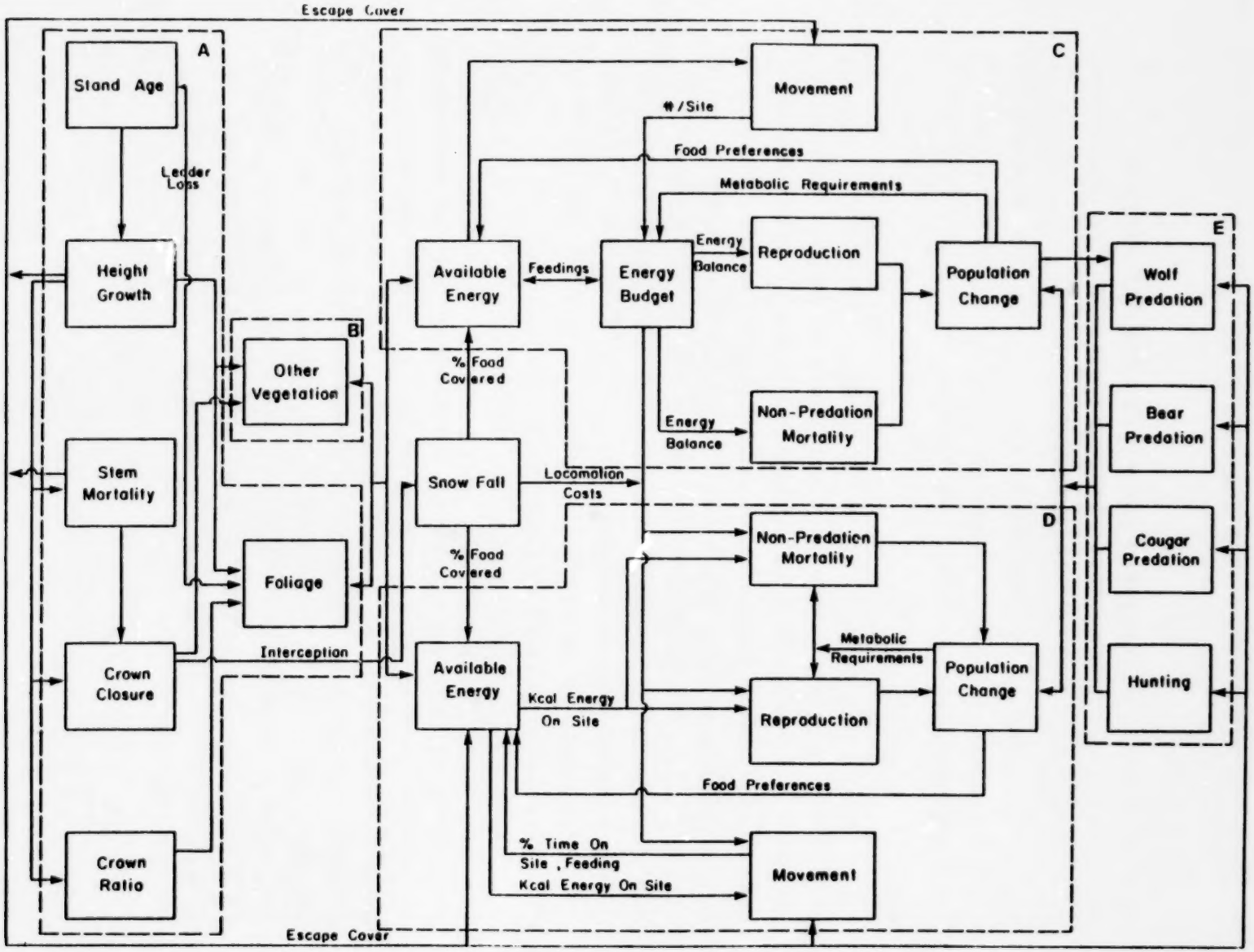


Figure 8.1 The conceptual model. A - Timber; B - Vegetation; C - Deer; D - Elk; E - Predation and Hunting.

Section 9 will define these conceptual and information needs as research hypotheses while emphasizing the importance of considering their interdisciplinary nature.

8.2.1 Vegetation

8.2.1.1 Competition

There was assumed to be no competition among understory species. This is clearly unrealistic. However, it may not be necessary to explicitly consider inter-specific competition among plants to evaluate the impact of changes in vegetation on deer and elk. A more detailed consideration of the effect of plant competition in the model on deer and elk populations should be pursued before the importance of competition can be assessed.

8.2.1.2 Forage Availability

The proportion of vegetation biomass that is available as food is presently assumed to be 10% of the standing crop of perennials and annuals and 13% of the standing crop of arboreal lichens. This is an oversimplification; the actual proportion will be species-dependent as well as a function of biomass and history of browsing (Noy-Meir, 1975). More accurate predictions of available food are necessary to examine more carefully any hypothesis of food limitation on deer and elk.

8.2.1.3 Effects of Silvicultural Practices

Again, if habitat is a crucial limiting factor to wildlife populations, a careful review should be done of the effects of silvicultural activities on habitat. Presently, silvicultural practices are assumed to simply change the biomass of vegetation. Long term effects are conceptualized in a crude and non-dynamic fashion. This conceptual gap is central to understanding effects of second-growth management on wildlife and should be investigated.

8.2.1.4 Alternate Representation of Vegetation

Twelve vegetation types are presently simulated. The static description of the vegetation submodel was time-consuming and prevented adequate discussion of vegetation growth, competition, and responses to timber growth, silvicultural practices and browsing, all potentially crucial research questions for the IWIFR Program. Important conceptual deficiencies could be better defined if an alternate structure could be derived for vegetation dynamics.

A simplification of the vegetation to 3-4 types would improve understanding of the interactions between vegetation and wildlife. One possible aggregation of species would be into grasses, forbs, shrubs, and lichen; certainly the first three may have similar growth responses to canopy closure (McConnell and Smith, 1970). Doubtless several other biologically realistic aggregations are also conceivable.

Such a compression of the vegetation would make it possible to examine clearly the critical interactions between elk and deer browsing and forage dynamics, and help define better experiments to test sensitive hypotheses concerning those interactions.

8.2.2 Timber

A better conceptual framework for predicting stand dynamics can certainly be constructed. However, the criterion to use in deciding what conceptual and information gaps exist in the present framework is that any improvements to conceptual understanding should enhance the ability to predict wildlife responses to forest structure, not the ability to predict commerical timber supply. Therefore, the conceptual and information gaps in the wood submodel discussed below refer only to those involving timber-wildlife interactions.

8.2.2.1 Effects of Animal Browsing

8.2.2.1.1 Mortality

Browsing is presently hypothesized to affect stem mortality and growth. The level of mortality is assumed to have a 1:1 relationship with the level of foliage consumption by wildlife. Alternate hypotheses (Figure 8.2) may reflect a more realistic biological representation. There is certainly evidence that the relationship is nonlinear for other herbivores with similar feeding patterns (Horn, 1971). The form of the relationship is also likely dependent on tree size. It may be Type 3 for very small trees, suggesting extreme sensitivity to foliage removal, and changes to

Type 1 as the tree matures, suggesting decreasing sensitivity to foliage removal with increasing size.

8.2.2.1.2 Growth

Browsing is presently assumed to only affect growth by retarding the rate of stand development. Furthermore, removal of conifer foliage is assumed to not ever halt stand development. Therefore browsing cannot permanently alter the characteristics of a tree. An alternate hypothesis is that browsing can permanently alter the characteristics of a tree (Figure 8.3). Again, regarding the wildlife as grazers of photosynthetic material, the permanent damage hypothesis is certainly a viable alternative (Shepherd, et al., 1979).

The two conceptual problems outlined above are crucial because wildlife are hypothesized to respond to a number of stand parameters such as density, height, and crown ratio (Sections 5, and 6).

8.2.2.2 Direct Effects of Wildlife

The effects of trampling and general physical disruption of young timber is presently not simulated. These processes probably affect the mortality of timber rather than it's growth. Trampling may break young stems or permanently bend them over, thereby removing them from the future stock of commercially valuable timber. Again, this impact is probably related to both tree size and animal density.

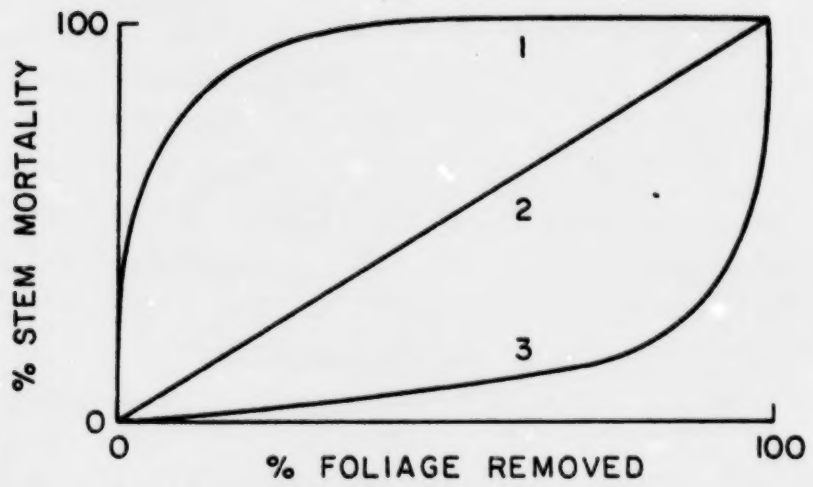


Figure 8.2 Alternate hypotheses about stand mortality response to animal browsing. (2) is hypothesis presently embedded in model; (1) and (3) are alternatives.

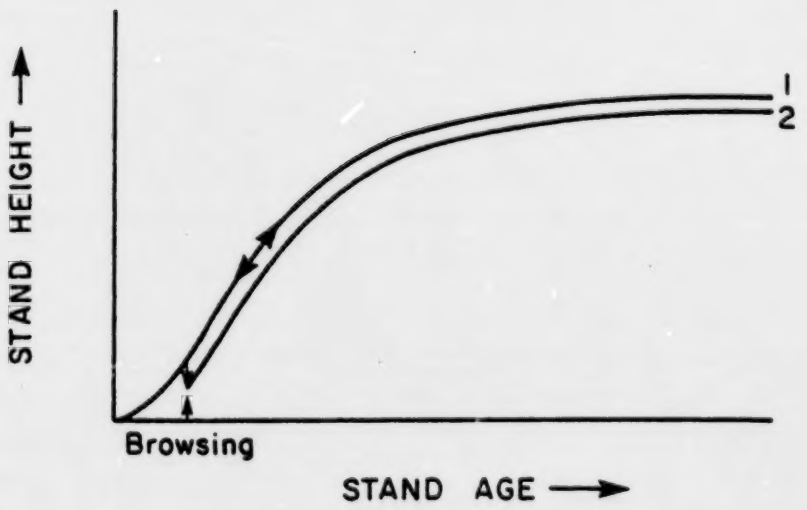


Figure 8.3 Alternate hypotheses about long-term effects of animal browsing. (1) represents hypothesis presently embedded in model; browsing simply retards development, not the tree characteristics; (2) is an alternate; browsing permanently changes tree characteristics.

8.2.2.3 Effects of Silvicultural Practices

Stem removal by juvenile spacing or commercial thinning is presently assumed to only affect crown closure. An implication of this hypothesis is that tree dimensions at a given age are the same for any stand density. Other forest growth simulators (Stage, 1973; Mitchell, 1972) consider the effect of stand density on variables that have been identified as important in the dynamics of elk and deer, such as height and crown ratio. This is a conceptual gap that will have to be filled to increase understanding of forestry-wildlife interactions.

8.2.2.4 Foliage Production

Foliage production is assumed to be a function of crown length. More realistically, it is probably a function of crown volume (Mitchell, 1975), or some other combination of tree attributes (Kimmins, pers. comm.). This information gap is crucial because browsing by elk and deer is tightly coupled to the relative biomasses of plants (Sections 5 and 6).

8.2.2.5 Influence of Other Vegetation on Timber

Competition between timber and other vegetation is presently hypothesized not to occur, or not to be important. This implies that the stand can always out-compete other vegetation and reduce its biomass by shading (Section 3.3). Participants stated that this was not always the case and that sufficiently dense vegetation can sometimes severely retard or completely halt growth of commercial timber species.

The question to be answered is: what is the influence of vegetation on the development of commercial timber? It is a conceptual gap which must be filled if understanding of wildlife responses to forest structure are to be improved.

8.2.3 Deer

8.2.3.1 Snow

8.2.3.1.1 Snow Interception

The current version of the model assumes that height does not affect a tree's snow interception capabilities provided the tree is greater than 2m tall. An alternate hypothesis is that larger trees will intercept more snow, given the same degree of crown closure in the stand.

Second, the assumption that 100% crown closure will result in complete snow interception, regardless of the amount of snow reaching the canopy, is unrealistic, at least for very heavy snowfalls.

Both of these assumptions effectively imply that sites with relatively young trees with dense canopies provide excellent winter range. This does not match with the perceptions of some workshop participants as to what constitutes good winter range.

8.2.3.1.2 Food Covered by Snow

The linear relationship between the depth of snow on the ground and the proportion of food of a particular type left uncovered implicitly assumes that food is distributed uniformly over the height of the plant. For most perennials

this is unreasonable since much of the lower parts of these plants are woody. For most food types available in winter this hypothesis implies that more food will be covered at a particular depth of snow than would actually be expected.

The sensitivity of the model to changes in this assumption has not been explored. Such an analysis would be worthwhile before allocating substantial effort to studying foliage height distributions for a variety of food species.

8.2.3.1.3 Effects of Snowfall on Lichen Availability

This interaction posed considerable conceptual difficulties due to the absence of a precise temporal sequence of snowfalls in winter. The linear relationship between snowfall and lichen availability may be reasonable as a first approximation but the duration of the heavy snowfall period may be equally, if not more important, in determining seasonal lichen availability. For example, it may be more reasonable to assume that during the heavy snowfall period, snowfalls occur frequently enough to effectively reduce lichen availability to zero while low snowfall periods may imply snowfalls infrequent enough to have no impact on lichen supply.

8.2.3.2 Movement

The basic conceptual question regarding movement concerns how deer select habitat. Considerable effort was devoted to conceptualizing this selection process. The problems faced in performing this conceptualization can be divided into three classes: timing of decisions, selection

criteria and spatial extent of concern.

First, it was assumed that the animals made their movement decision at the start of each season. This is probably reasonable for spring and summer, since deer appear to demonstrate fairly high fidelity to particular regions during those times of the year. However, in winter this assumption (as discussed in Section 5.3.1) implies that the animals select habitats before knowing how severe the winter will be. In other words, deer distributions are not affected by snowfall. More information is needed to decide whether deer do actually move in response to changes in snowfall.

Second, the selection criteria which the deer use to evaluate the potential of different areas as habitat may be too simple. For example the escape cover criterion does not include debris or understory vegetation as components, while the feeding habitat criterion assumes that all food types are equally important in determining a site's value, irrespective of deer preferences. In addition the method of weighting and aggregating the criterion for each site may be conceptually inadequate. It may be more reasonable when calculating the value of a four-site block to consider only the site with the highest value for each criterion. For example, if a single site comprises excellent winter range but is lumped with three other sites having poor winter range (i.e., no trees greater than 2m), the overall winter range value of that block might be unrealistically low.

This problem is linked to the third class of conceptual problems related to deer movement. Is a block of four sites (total area - 320 ha) a reasonable representation of the "sphere of operation" of a deer during an entire season, or do deer consider an area larger (or smaller) than

this in evaluating a particular site? The observed relatively high fidelity of deer to a particular site within a season suggests that one need not consider larger areas. However, this question needs to be evaluated more carefully since it has important implications to the overall conceptualization of the deer model.

8.2.3.3 Feeding

The quantities used to convert total annual new growth into seasonal caloric abundance of each food type (Table 5.3) deserve more attention than they received during the workshop. Some values were simply guessed at due to time constraints and should be carefully reviewed to ensure their accuracy.

The list of relative preferences for the 14 food types (Table 5.4) was developed from information on the incidence of these food types in deer rumen. Such information clearly reflects the interaction between preference and availability of food and will be badly biased unless all food types were equally abundant when the deer were feeding.

True preferences are difficult to establish without careful experimentation. However, knowledge of such preferences and how they differ among food types is central in determining the level of detail at which vegetation must be considered to understand the consequences of deer-food interactions (Section 8.2.1.4).

8.2.3.4 Survival and Reproduction

The population dynamics of deer in the model are extremely sensitive to changes in the energetics-survival and energetics-natality relationships described in Sections 5.4 and 5.5. All other processes described in Section 5 affect deer populations only through these two relationships. Much attention should be focussed on carefully assessing the hypotheses that went into developing these relationships as well as the accuracy of their parameters. The sensitivity of deer survival to winter energy deficits is of particular importance.

8.2.4 Elk

8.2.4.1 Escape Cover

A critical assumption in the hypothesized influence of escape cover is that elk require escape cover to be present before they will forage in an area. An alternate, equally viable hypothesis is that elk prefer areas with adequate escape cover but will use any area that has adequate forage if forage is limiting. These are two extreme hypotheses, and combinations of them are equally feasible. Elk may continually tradeoff between the value of cover and forage.

A more basic consideration is the conceptualization of escape cover as a function of timber density and height. This hypothesis implies that understory vegetation and debris do not contribute to escape cover. Thick undergrowth of herbaceous vegetation or high debris levels may in fact provide good cover for elk, especially the younger, smaller age-classes. Thomas et al. (1979) have found debris to be an important component of escape cover.

The attributes of the timber in a stand which were hypothesized to define escape cover may be improper. It is difficult to imagine, for example, that 80 35m tall trees/ha provide equally good escape cover as 1000 2.5m tall trees/ha.

The conceptualization of escape cover, both its definition and its importance to elk in selecting habitat, must be critically examined.

8.2.4.2 Food Availability

It was hypothesized that elk use levels of available food energy to partially determine movement. Available energy was assumed to include the concepts of food preference and seasonal foraging habitats. It embodied the bias that elk preferences, as measured by their selection of foods and environments, reflects their requirements, or ingrained habits. Alternatively, as in the escape cover hypotheses, elk may only be doing what they prefer to do. Necessity may force radical changes in their diets but not incur any appreciable detrimental effects.

Very simply, the concept that food availability is critical in determining elk movement and distribution patterns must be closely examined.

8.2.4.3 Survivorship and Fecundity

The survivorship and fecundity relations (Figure 6.4) were meant to capture the hypothesis that food densities could adversely affect elk population dynamics. The hypothesis

is that forage density, integrated over a relatively large area, is an appropriate index of forage value. An alternate hypothesis is that the distribution of food in the environment may be the critical factor. For example, a pocket of dense, high quality forage may be far more valuable to elk in terms of survivorship and fecundity, than a large total biomass of low density, evenly distributed forage.

8.2.4.4 Emigration

Alternate hypotheses about immigration and emigration could dramatically affect predictions of the dynamics of an elk population. At present, an arbitrary carrying capacity is used to prevent the buildup of a large density of elk in the watershed. Total population density is assumed to be the only determinant of elk emigration from the watershed. But, relative food availability per elk may be a more biologically realistic indicator than simple population size. Unfortunately, experiments to test the sensitivity of this hypothesis would be expensive and time consuming.

8.2.5 Predation and Hunting

8.2.5.1 Seasonal Distribution of Predation

Seasonal predation is calculated by allocating annual predation rates to the three seasons using the fixed proportions in Table 7.1.

The weakness of this approach is that the annual rate is calculated based on the prey population size immediately after fawning and calving seasons. The seasonal rates are not sensitive to the actual seasonal population sizes.

If some process other than predation reduces a prey population, the model does not adjust the amount of predation to reflect the change because the all-seasonal rates are based on the population size at the beginning of the summer. An improvement in understanding will be gained by developing relationships that predict seasonal predation rates from seasonal prey densities.

8.2.5.2 Functional Responses

All of the functional responses discussed in Section 7.0 were "best guess" hypotheses. Before much faith can be put in these hypotheses, data needs to be gathered in the field or retrieved from the available literature. Both the assumptions about density dependence or independence and the specific parameters were not based on strong evidence.

8.2.5.3 Numerical Responses

All of the numerical responses discussed in Section 7 were "best guess" hypotheses. Before much faith can be put in these hypotheses, data needs to be gathered in the field or retrieved from the available literature. Both the assumptions about density dependence or independence and the specific parameters were not based on strong evidence.

8.2.5.4 Wolf Predation

8.2.5.4.1 Functional Responses to Deer

The hypothesis underlying the functional responses to fawn and adult densities (Figure 7.1) are quite complex. The complex nature of these hypotheses can be illustrated by comparison with a set of simpler hypotheses (Figure 8.4). These simpler hypotheses state that at high densities of both fawns and adults the predators become saturated and the ratio of fawns to adults in the total kill becomes constant. At lower densities the predators cannot satisfy their requirements from the combined sources of fawns and adults and both functional responses decline as densities decline. The actual slopes of the curve depend on the fawn to adult ratio in the populations. The solid line in Figure 8.4 represents a higher fawn-adult ratio than the dotted line.

To generate the functional response to adults shown in Figure 7.1b from the relationship shown in Figure 8.4b it was necessary to assume that there exists a range of densities where a decrease in the density of both adults and fawns will result in a reduction in predation on fawns which will be compensated for by increased predation on adults. This assumption is manifested as the humped response of Figure 7.2b. The exact mechanism that would generate such a response is unclear.

To generate the S-shaped functional response to fawns shown in Figure 7.2a from Figure 8.4b, it was necessary to assume a switch from deer to elk and other food sources at low densities. It was hypothesized that a tendency towards larger packs would be necessary to increase predation pressure on elk.

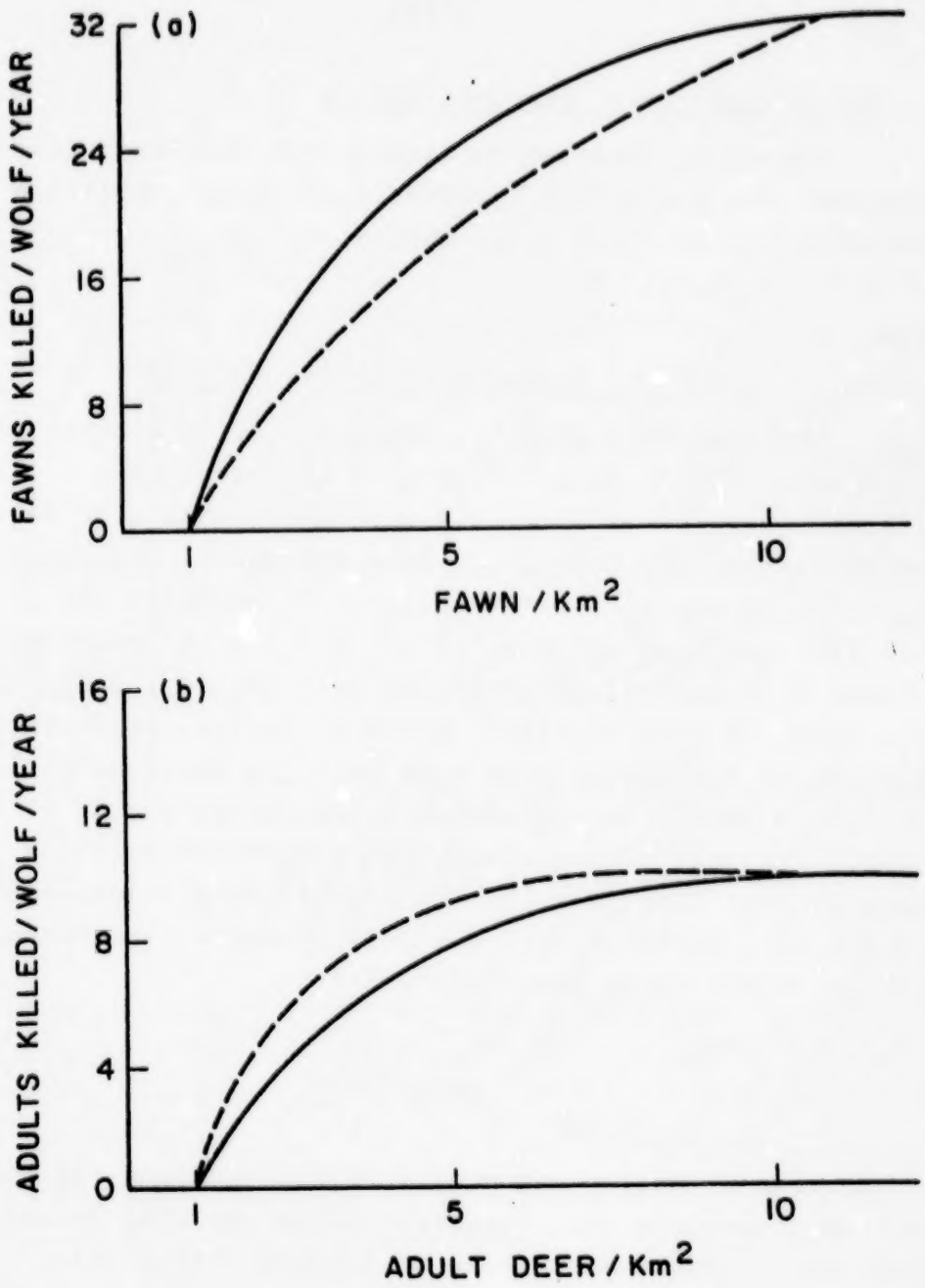


Figure 8.4 Alternate hypotheses about functional responses of wolves to deer. The solid line represents a high fawn-adult ratio, the dotted a low fawn-adult ratio.

8.2.5.4.2 Functional Response to Elk

Wolves are assumed to feed on elk only when deer densities are low. This hypothesis was based on little understanding and must be reconsidered.

8.2.5.4.3 Numerical Response of Wolves to Deer

The numerical response (Figure 7.3) is another complex hypothesis that is best illustrated by postulating a simpler alternate hypothesis (Figure 8.5). The simple hypothesis states that as the density of deer increases, the density of wolves increases proportionally. To generate the numerical response (Figure 7.3) from the alternate hypothesis (Figure 8.5), it was necessary to hypothesize the existence of a range of deer densities where the wolves would show no response to increasing deer density. The exact mechanism for lack of response is unclear. In the model, it is directly related to the assumption that there exists a range of deer density where the wolves' food requirements are met by a diet composed entirely of deer. Whether such a range exists is an open question.

8.2.5.5 Bear Predation

Bear predation was simply represented and the hypothesized relationships were best guesses. Bears may prey on animals other than fawns and at times of the year other than summer. The present functional form for bear predation and the kinds of wildlife bear prey upon must be closely examined.

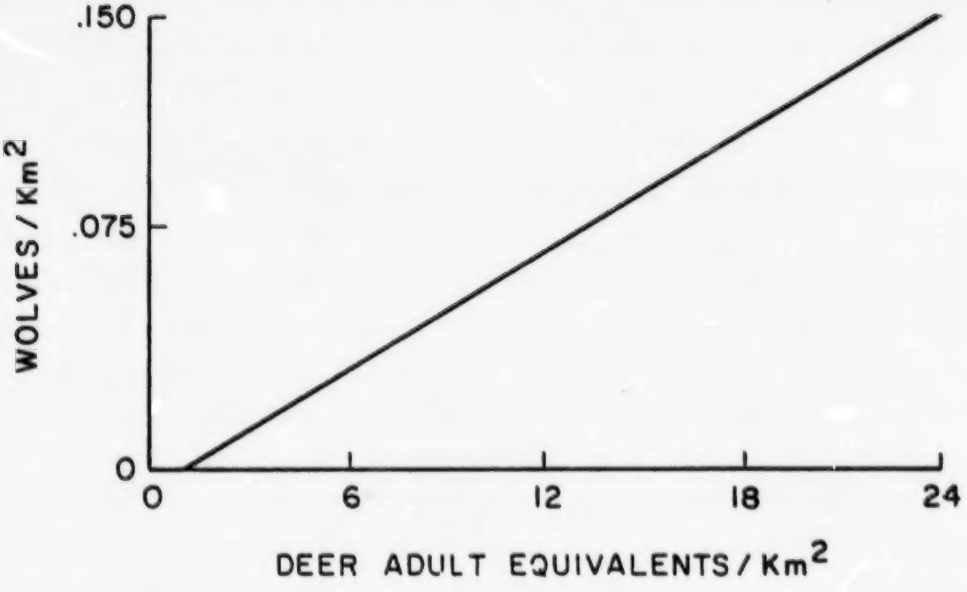


Figure 8.5 Alternate hypothesis about the numerical response of wolves to deer.

8.2.5.6 Cougar Predation

The conceptual gaps in the process of cougar predation are the same as those for bear predation. This oversimplification in the case of cougars is a major weakness because of the magnitude of cougar predation on deer. The entire area of cougar predation represents significant conceptual gaps in understanding.

8.2.5.7 Predator-Predator Interactions

The model assumes that there is no interaction between predators. While some concern was raised over the possible interactions between wolves and cougars, there is little evidence to support hypotheses about such interactions. Information on this area of the predator question is completely absent; its importance is unknown.

8.2.5.8 Hunting

The dynamics of hunters were not explicitly considered in the hunting relationship. The harvest rate relationship developed (Figure 7.7) made gross assumptions about the behavioural responses of hunters to deer density. This relationship represents a best guess hypothesis and must be reconsidered.

8.2.5.9 Escape Cover

The concept of escape cover is poorly defined and the effect of escape cover on the vulnerability of prey to predation and hunting is poorly conceptualized. The index of vulnerability used in the model is based on an aggregate measure of the proportion of the area that is suitable escape cover. This index affects the number of animals that are available to predators.

The Holling (1959) disc equation offers insight into how vulnerability may affect predation:

$$A(N_o) = \frac{T_t a N_o}{1 + aT_h N_o}$$

where N_o = prey density,

$A(N_o)$ = number of attacks per predator,

T_t = total time predator and prey are exposed,

a = rate of successful search, and

T_h = time spent handling (pursuing, capturing and eating) each prey.

Changes in escape cover can modify the functional response (Figure 8.6) in three ways.

1. The prey density (N_o) can be defined as vulnerable prey as was done in the model;
2. the rate of successful search (a) can be modified to reflect the difficulty a predator has in finding prey; or
3. the handling time (T_h) can be modified to reflect the difficulty a predator has in pursuing and capturing prey.

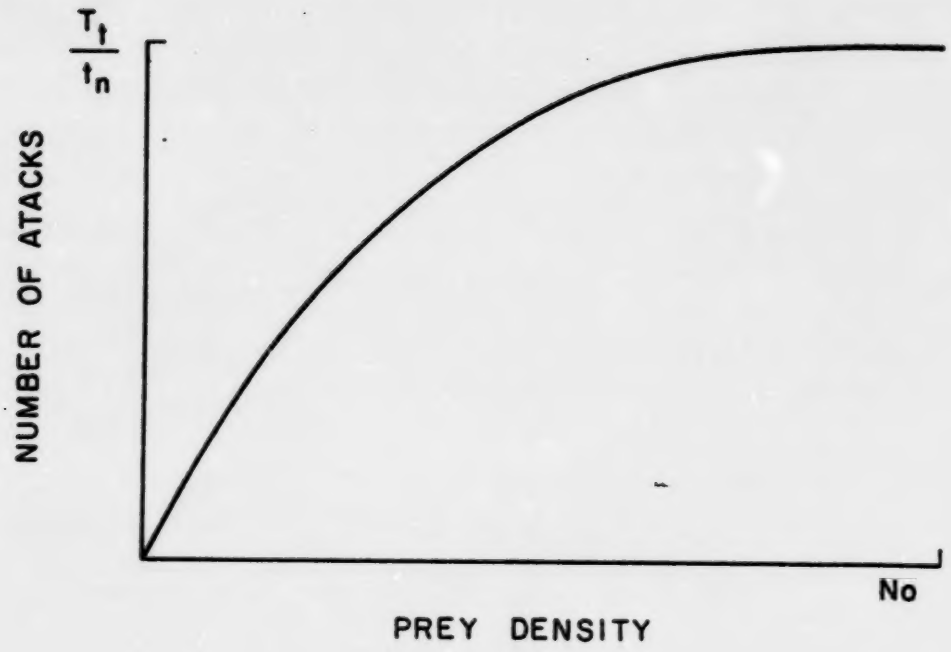


Figure 8.6 Predator functional response to prey density as expressed by the disc equation.

Changes in prey density (N_o) and in the rate of successful search (a) will both modify the slope of the functional response at low prey densities and changes in handling time (T_h) will affect the maximum rates of attack as well as the slope.

A detailed examination of the specific predator-prey systems is needed to carefully formulate hypotheses about the effect of escape cover on the functional responses of predators.

8.2.5.10 Predator Population Dynamics

A major missing piece of the puzzle is an understanding of the population dynamics of predators and hunters. To fully understand the predator-prey systems it may be necessary to include the population processes (birth, mortality, reproduction) for the predators. However, it is not clear that the behaviour of the model would be qualitatively different or that the research planning objectives would be better served by including predator population dynamics.

8.3 Model Behaviour

Three scenarios were simulated on the last day of the workshop: a baseline scenario, representing a simulation of existing forestry management regimes for each site and the unmanaged dynamics of wildlife and their predators; a "tree farm" scenario, in which the goal was to maximize flow of commercial timber from the area; and a "wildlife farm" scenario, in which the goal was to maximize production of deer and elk from the area. Because of the extreme

effects of predation on wildlife populations, these three scenarios are presented below without predation. A fourth scenario showing the effects of predation is presented at the end.

Output from the workshop model simulations is useful because it provides a focus for discussion and evaluation of the model and hypotheses. However, exact numerical output is not important because the model is still crude and preliminary. It is more useful to examine changes in trends of variables under different management actions and hypotheses.

8.3.1 Baseline Scenario

Input conditions for this scenario are given in Figure 8.7. One site per year was harvested; the specific site was chosen at random from the potential candidates.

The annual harvest of wood (Figure 8.8) shows a mean removal of about 70,000 cubic meters. The fluctuations in the harvest come from commercial thinnings and the fact that stands are not harvested immediately upon reaching 36m in height. If not harvested they keep accumulating height and therefore volume. The large dip at about year 15 is because no sites were 36m in height that year and the peak in about year 20 is because there were a large number of sites commercially thinned that year.

Deer populations increase consistently from their initial starting value of 450 animals and reach 4000 animals in 30 years, about an 8% increase per year (Figure 8.9). Food never becomes limiting to deer, even at the high levels reached in the later years. This is likely due to the absence of density-dependence in the deer feeding processes (Section 5)

Site Preparation

```
0 1 0 0 0 0 0 0 0 1 0 1
0 1 0 0 0 1 0 0 1 0 1 0
0 1 0 1 0 1 0 1 0 1 0 1
1 0 1 1 1 0 1 1 1 1 1 1
1 0 0 1 1 0 1 1 1 1 1 1
1 1 0 1 0 1 0 1 0 1 0 1
1 0 1 0 1 0 0 1 0 1 0 0
1 1 1 1 0 1 0 0 1 0 0 1
```

0 - no site preparation
1 - burning

all harvested sites are planted

Initial Stand Age

```
M M M  0  20 20 40 45 50 50 50 50
M M  0 15  0 30 45 45 55 55 55 55
M M  5  5 20 40 55 55 60 60 60 60
M M 10  5 30 45 55 60 60 65 65 70
M M M  M  30 40 55 60 60 65 65 70
M M M  M  20 40 55 55 60 60 60 60
M M M  M  10 40 40 50 50 50 55 55
M M M  M  10 20 30 30 30 45 45 45
```

M - mature

Tending and Harvest

```
3 3 3 3 1 1 1 1 1 2 2 2
3 3 3 1 1 1 1 1 2 2 2 2
3 3 1 1 1 1 1 2 2 2 2 2
1 1 1 2 2 2 2 2 1 2 2 3
1 1 1 2 2 2 2 3 2 2 2 3
1 1 1 1 1 1 1 2 2 2 2 2
3 3 1 1 1 1 1 1 2 2 2 2
3 3 3 1 1 1 1 1 1 2 1 2
```

1 - space at 6m to 375 stems/ha
    harvest at 36m
2 - space at 6m to 500 stems/ha
    thin at 25m to 250 stems/ha
    harvest at 36m
3 - harvest at 36m

Figure 8.7 Initial site conditions for baseline scenario.

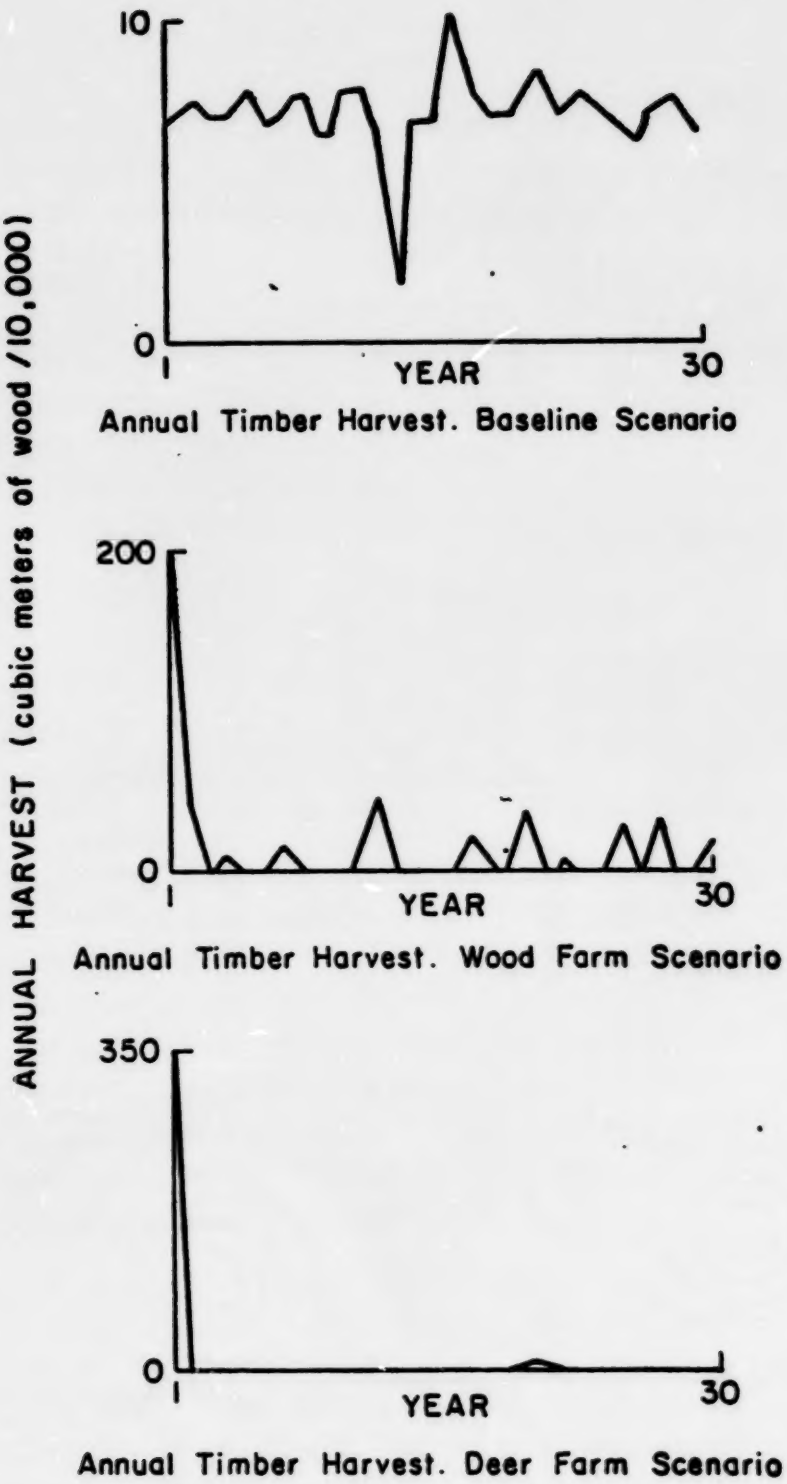


Figure 8.8 Woods harvest trends under three senerio

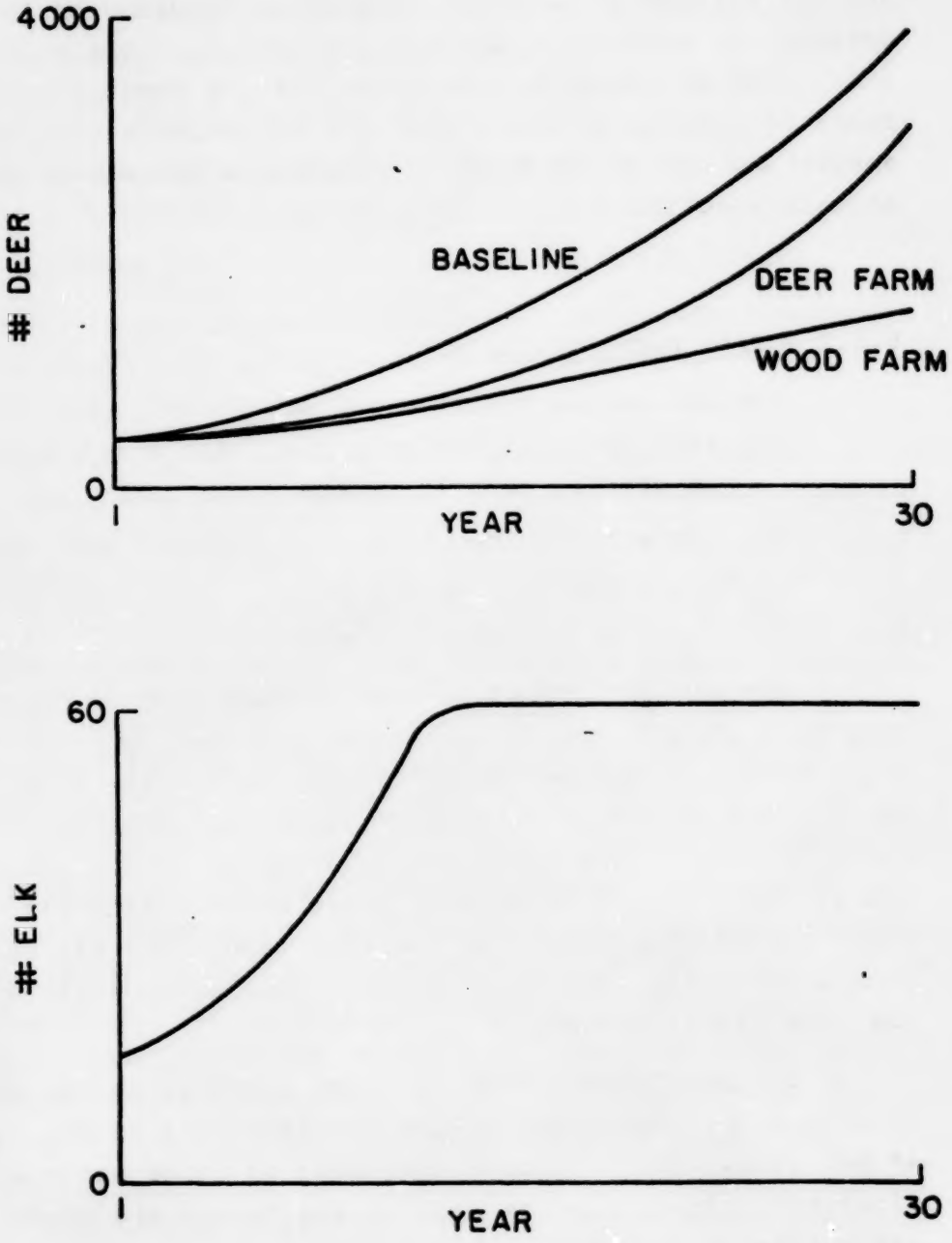


Figure 8.9 Deer and elk population trends under three scenarios. Elk show the same trend in all three model runs.

and the absence of negative effects of browsing on the dynamics of vegetation species (Section 3). Elk populations also increase steadily from their initial population and reach 60 animals at about year 15; the animals then begin emigrating out of the area to maintain a maximum of 60 animals (Section 6).

8.3.2 "Tree Farm" Scenario

The conditions for this scenario are:

(a) each year, harvest all sites for which the height is greater than 36 meters;

(b) apply herbicides to all sites clear cut; and

(c) space and thin on every site, according to the rules in the baseline scenario.

The annual harvest of wood (Figure 8.8) shows a very high initial volume extraction followed by periodic heavy bursts of harvesting every 2-5 years. The high initial extraction is because of the clear cutting of mature stands in the upper and lower parts of the watershed. The periodic bursts of harvest occur because many sites reach harvestable height at the same time. The harvesting rule effectively temporally synchronizes those sites with the same growth indices.

Elk populations show the same trend as in the baseline (Figure 8.9). Deer populations increase at a slower rate, 4% per year. The herbicide treatment of large numbers of sites effectively removes much of the forage and browse that was available in the baseline scenario.

8.3.3 "Wildlife Farm" Scenario

The conditions for this scenario are:

(a) all sites are initially mature;

(b) each year, harvest all sites for which the height is greater than 3m; and

(c) allow natural regeneration on all cut sites.

Participants specified particular sites not to be harvested throughout the simulation and a tending regime different than that in the baseline.

Annual harvest of wood (Figure 8.10) again shows an initial large extraction of timber followed by effectively no volume yield. Again, in the first year, many mature sites were harvested. Sites are still being harvested in succeeding years but volume yield is very small because trees are only 3m in height when cut (Figure 4.3).

Elk again have dynamics similar to those in the baseline. Deer populations respond almost as well as in the baseline scenario and reach a population size of about 3000 by year 30 (Figure 8.9). Food is likely abundant because of natural regeneration, the absence of site preparation and higher proportion of sites with low relative timber foliage biomass. The lower final population suggests that the conceptualization of deer movement may be such that they are not responding well to favourable changes in their habitat. They may not be taking sufficient advantage of the improved habitat that is created for them by the simulated forestry management regimes. This suggests that the processes involved in deer movement and re-distribution are poorly understood.

Harvest

```
0 0 1 0 1 0 1 0 1 0 1 0
1 1 1 0 0 1 0 0 1 0 1 0
1 0 1 0 1 0 0 1 0 0 1 1
1 0 1 0 0 1 0 1 0 0 1 0
1 1 0 1 0 0 1 0 0 1 1 1
1 1 1 1 1 1 1 0 0 0 0 1
0 1 0 1 0 1 0 1 0 1 0 0
0 1 0 1 0 1 1 1 0 1 1 1
```

0 - never harvest
1 - harvest when height 3m

Figure 8.10 Input conditions for "wildlife farm" scenario.

An alternative explanation for the reduced deer population may derive from snow effects. The increased food supplies generated by this "wildlife farm" scenario may be compensated for by the fact that most of this food is being produced on sites that provide poor winter range. In other words, overall winter food supplies may actually be reduced as a consequence of greater snow depths on most sites. Since winter feeding is important to both survival and natality of deer the effect would be a reduction in population growth rates.

8.3.4 Predation Scenario

Conditions for this scenario are the same as those for the baseline scenario (Section 8.3.1) except that all predators have been included.

Elk and deer populations decrease to very low levels quickly and remain low for the duration of the simulation (Figure 8.11). Wolf numbers decline as prey decline (Figure 8.11). This behaviour is extremely different than that in all other scenarios and strongly suggests that, given the manner in which the predation processes were conceptualized (Section 7) the population dynamics of deer and elk are highly sensitive to predation.

8.4 Model Refinements

The present model is very complex and therefore difficult to interpret and understand without extensive gaming. We strongly recommend a thorough analysis of the concepts and data used to develop the present model. Initial

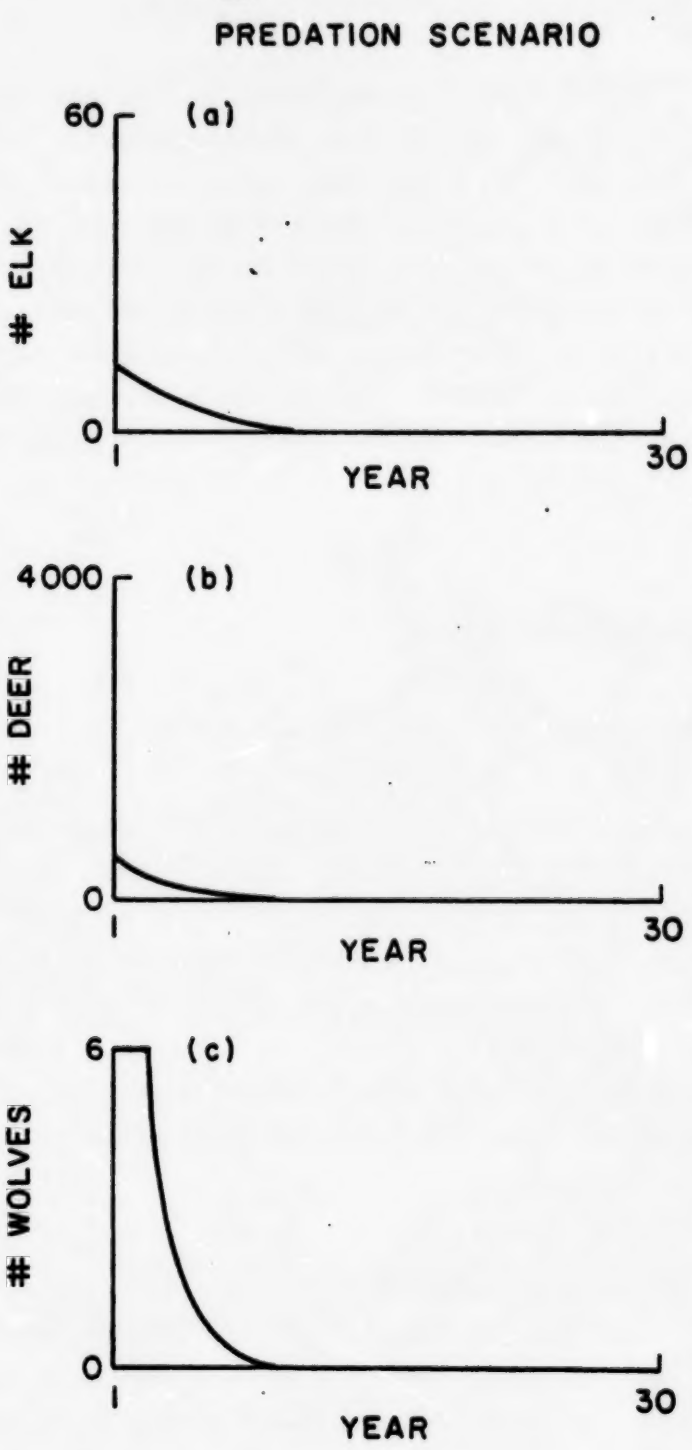


Figure 8.11 Model behaviour for predation scenario.

literature reviews are often very helpful in filling many of the data and parameter uncertainties, as well as some conceptual deficiencies.

We recommend against making refinements which add to model complexity until the dynamics of the current version are well understood. Perhaps a careful analysis of the current model will show that far less detail is sufficient to understand the interactions between forestry and wildlife population dynamics. The refinements detailed below either require new conceptualization of existing parts of the model, addition of important components that were left out of the initial model, or the acquisition of better data.

8.4.1 Vegetation

There appears to be little effect of food limitation on deer and elk from the predictions of the model presented in Section 8.3. Therefore there is no present need to refine the conceptual structure of the vegetation submodel. Future refinements to the deer and elk models that produce food limiting effects will also provide guidance as to what refinements are needed in the vegetation submodel.

8.4.2 Timber

8.4.2.1 Effects of Browsing

The model will have greater predictive power when the effects of browsing on tree growth and mortality are better quantified. Alternately, equally viable hypotheses exist for the impact of foliage removal. These relationships can be easily measured with simple artificial defoliation experiments (e.g., Craighead, 1940).

8.4.2.2 Direct Effects of Wildlife

The model presently does not consider the direct effects of wildlife on timber. This conceptual deficiency can be removed by developing a relationship that predicts direct removal of stems as a function of stem size and use of a site by deer and elk, as measured in number of animals/unit area/unit time. The time factor is crucial because increasing duration of stay in a site probably results in greater physical damage to the young conifers on that site.

8.4.3 Deer

Some of the potential model refinements suggested by the discussion of conceptual and information gaps in the deer submodel (Section 8.2.3) would be difficult to make with the present model structure. For example, improving the prediction of food covered by snow would entail a vegetation submodel much more detailed than the one at present. Given the absence of food limitation, even with probable underestimation of winter forage availability (Section 8.2.3.1.2), this part of the model is not worth refining at present. However, some parts of the deer model could likely be easily improved.

8.4.3.1 Snow Interception

The degree of snow interception is related to easily measured variables such as crown closure and crown length. Accurate relationships for predicting snow interception can likely be derived using variables already calculated

in the present model; such relationships would be easy to implement.

8.4.3.2 Food Preferences

The estimation of unbiased preferences is a difficult task but, if it were done, could be very simply refined in the model. A review of existing literature would be a prudent step because the preferences may already be documented.

8.4.3.3 Exploitation

Exploitation competition was not included in the first version of the model and one form of this process is presently included. It has no qualitative effect on model behaviour. Yet, other forms of exploitation could be simulated, using competition models from classical predator-prey theory (e.g., Griffiths and Holling, 1969). The model may be sensitive to other alternate hypotheses about exploitation, thus pointing to the need for research in that area.

8.4.4 Elk

8.4.4.1 Escape Cover

If what elk perceive as good escape cover can be quantified, the model can be refined to accommodate those changes. Additional variables which elk probably use as escape cover, such as debris and vegetation, are simulated

in the present model and appropriate relationships could be developed to relate these variables to the escape cover value of a site.

8.4.4.2 Food Preferences

See Section 8.4.3.2, Deer Food Preferences. The arguments are the same.

8.4.4.3 Emigration

The variables which initiate emigration are likely to be difficult to measure and are probably similar to those which initiate movement between sites within a region. The present hypothesis implies that elk are intolerant of physical crowding, irrespective of the range value for the area. The model will have greater predictive power if the proper mechanisms for emigration can be described.

8.4.5 Predation and Hunting

8.4.5.1 Seasonal Distribution of Predation

The predation rates in the model are not sensitive to seasonal changes in prey density (Section 8.2.5.1). The functional responses can be redefined to operate seasonally.

8.4.5.2 Functional and Numerical Responses of Predators to Prey Density

All of the functional and numerical responses were best guess hypotheses. These hypotheses need to be evaluated by examination of existing data and available literature. This is necessary if the parameters and form of the relationships are to achieve a measure of credibility. However, the use of biologically realistic models for predation ensures that any refinements can be made very simply.

8.4.5.3 Wolf Predation

Predation by wolves on deer and elk received the most attention in the development of the predation submodel. Predation is represented by a set of tightly linked hypotheses about the functional responses of wolves to fawns, adult deer, and elk; and numerical responses of wolves to deer. The conceptual adequacies and inadequacies are discussed in detail in Section 8.2.5.4. Better parameter estimates can certainly be derived from existing wolf predation literature (e.g., Haber, 1977) and used to improve this part of the model.

8.4.5.4 Cougar Predation

Each cougar may kill as many as 50 deer per year. This rate is significantly higher than the number of kills per wolf. However in the model cougar predation received a highly simplified treatment. Much more thought is required before a good understanding of cougar predation can be included in the model. In view of the assumed impact

cougars on deer and elk this part of the model should be refined.

8.4.5.5 Escape Cover

A major question is, how does change in the amount and availability of escape cover effect predation? The problems with the current conceptualization were outlined in Section 8.2.5.9. A rationale needs to be developed to support hypotheses about which components (availability of prey, successful search rate of predators, handling time) are affected by escape cover. Because escape cover is closely tied to various silvicultural and forest practices the development of a better understanding of the effect of escape cover is a prime candidate for model refinement.

9.0 RESEARCH RECOMMENDATIONS

9.1 The Importance of Interdisciplinary Hypotheses

The IWIFR Program spans two broad disciplines: forestry and wildlife biology. The interdisciplinary nature of the program makes research planning a difficult task. Links between disciplines must be understood in interdisciplinary research planning and data collected by one discipline should be useful to other disciplines. Researchers involved in interdisciplinary research must broaden their outlook to the "whole system" level from the more conventional "subsystem" or "single discipline" level.

But establishing hypotheses that consider all relevant disciplines is difficult without an organizational format. The simulation model developed in an AEAM workshop provides that format in terms of a set of linked hypotheses about system behaviour. The model developed in the IWIFR reseach planning workshop embodies a set of hypotheses about the interactions among forest vegetation, deer, elk, predators and man. This section explicitly identifies those hypotheses which should be given further attention. We have attempted to include only those hypotheses whose testing will provide valuable contributions to the objectives of the IWIFR project. These hypotheses have been chosen on the basis of their impact, both observed and anticipated, on the model's behaviour. The more sensitive the model's predictions are to changes in a particular hypothesis, the more important it is that the hypotheses be tested.

It is critically important to recognize that research on any of the hypotheses will benefit enormously from an interdisciplinary approach. In particular, the careful design

of an experimental forest management plan to provide an arena for evaluating deer, elk and predator responses to a variety of management actions would constitute an invaluable tool for the IWIFR program. Designing such a plan would only be worthwhile if inputs from all relevant disciplines were encouraged. Allocation of a small watershed in which all the field research were carried out would help to ensure interdisciplinary coordination and understanding.

9.2 Vegetation

The vegetation submodel is rich with parameters. Most of these numbers were estimated under the pressure of time. It would be prudent to review these parameters to reveal large inaccuracies.

9.2.1 Competition

There is no competition among vegetation species. This hypothesis is probably invalid. However, competitive interactions among plants should only be explicitly considered insofar as they are influenced by deer and elk feeding. The effects of browsing pressures on plant population dynamics deserves much more attention than it was given in the workshop.

9.2.2 Forage Availability

10% of the standing crop of all vegetation is available as forage to deer and elk. This hypothesis should be carefully reconsidered to evaluate the extent to which plant type, browsing history and standing crop affect forage availability.

9.3 Timber

9.3.1 Browsing Effects

The relationship between tree mortality and animal browsing is strictly linear. This is certainly not true for grazing effects on conifers from other herbivores (e.g., forest insects).

Tree mortality from animal browsing is independent of tree size. The tight coupling between regeneration stand dynamics and wildlife grazing indicates that this hypothesis should be tested. This and the above hypothesis are very closely linked and can be tested together in the same field project, given an appropriate experimental design.

Animal browsing does not permanently change those characteristics of a stand which are important to wildlife (crown closure, average height, crown ratio, etc.). An experimental approach to testing this hypothesis is beyond the temporal scope of the IWIFR program, but can be examined by constructing a more appropriate and realistic conceptualization of stand dynamics.

9.3.2 Direct Effects of Wildlife

Wildlife does not directly affect tree and stand growth. Trampling may cause high stem mortality. A simple field experiment could be designed to measure the stem loss under a range of deer and elk use levels and tree sizes.

9.3.3 Competition From Other Vegetation

Timber dynamics are independent of understory vegetation. This assumes no competition between commercial wood species and other vegetation, an assumption which may be invalid in some situations. Some participants at the workshop recalled cases in which regeneration of commercial timber species was unsuccessful because of heavy growth of other plants. This hypothesis can easily be tested in a field project by measuring tree growth rates under various biomasses of other vegetation.

9.4 Deer

9.4.1 Snow

The effect of snowfall on food supply and energy costs for deer is independent of the actual sequence of snowfall events during winter. This hypothesis may be best evaluated in a theoretical framework since field experimentation would be very difficult and likely only correlative. Using the model to examine responses to changes in the temporal "structure" of winter should provide insights into how detailed an understanding of the interactions between snowfall patterns and deer survival is necessary.

For all trees greater than 2m tall, there is a direct relationship between crown closure and snow interception, with complete interception occuring at 100% crown closure. This is likely not true; however, it provides a null hypothesis against which the interactions between tree height, crown closure and snow interception can be evaluated. Such interactions lend themselves easily to field measurements in managed

stands and may provide valuable insights into the characterization of winter range.

The relationship between snow depth and the proportion of food available to deer is strictly linear. The assumption implicit in this hypothesis, that the food-height distribution for all plants is uniform, deserves attention. If this assumption is seriously invalid for important winter food species it will severely overestimate the detrimental impact of snowfall on deer survival. Information on this presumably can be found in the literature and field analyses may be unwarranted - the resolution required is not great.

9.4.2 Movement

Deer select winter range habitats at the beginning of winter and do not modify their distribution in response to the actual snowfall patterns that winter. Observations of habitat fidelity during winter would provide useful information on the validity of this assumption. It is possible that the costs of redistribution when snowfall is unusually heavy may outweigh the benefits of moving to more suitable winter range. If this is not true the deer in the model may be more sensitive (in terms of effects on survival) to variations in winter climate then would be expected in reality.

The components used to characterize the value of a site as deer habitat are sufficient to accurately reflect the utility of that site as winter range, escape cover habitat, and feeding habitat. This hypothesis needs more discussion. It is difficult to conceive of simple field experiments to effectively identify the critical components of deer habitat. A concerted effort should be made to carefully identify a list of components which are most likely to be important.

From such a list, predictions of deer distributions in a particular area at different times of year could be compared to the actual seasonal patterns in that area.

An area of 320 hectares is a reasonable approximation of the range of movement of an individual deer in a particular season. This hypothesis is related to the one above. Again, observations of within season movement patterns would provide useful information for the testing of this hypothesis.

A great deal of emphasis was placed at the workshop on the importance of spatial heterogeneity to deer survival. Situations such as the juxtaposition of good winter range with a winter food supply were thought to be critical to deer. Clearly, this question is one of the central issues of the IWIFR program. A great deal of careful thought and discussion must be devoted to developing ways of evaluating just how sensitive deer are to the structure of the meso-environment which surrounds them. Presumably, the more mobile (both in terms of capacity and willingness to move) the animals are, the less important local disturbances become. Studies of deer movements in response to changes in habitat should probably form the focus of research effort concerned with deer. Studies of deer distribution and abundance carried out in conjunction with experimental forest harvesting and second growth management practices would be especially useful.

9.4.3 Feeding

Both the annual biomass to seasonal kcal conversion factors and the relative preference values used in the model should be carefully reviewed to ensure that they are reasonable.

Research aimed at establishing the actual deer preferences for various food types might be worthwhile, although the effort required to generate accurate results may outweigh the benefits. Educated guesses at preferences derived from the literature and perhaps some crude measures of electivity (Ivlev, 1961) should be sufficient. It is important to recognize that only large differences in preference are worth considering. Two species which exhibit only a 20% difference in preference might well be considered a single food type from the deer's point of view.

There is no interference competition for food among deer and exploitation effects are only important at very high deer densities relative to their food supply. These two assumptions imply that the deer are efficient, cooperative foragers and have important implications to both deer and their food supply when deer populations become very large. The absence of these effects presumably accounts to some extent for the extremely large deer populations observed in all model scenarios without predation.

9.4.4 Survival and Reproduction

All mortality except that due to predation and hunting occurs during winter and is influenced solely by a winter energy budget.

Reproduction (birth of fawns) occurs at the beginning of summer and is influenced solely by winter and spring energy intake.

These two hypotheses were considered quite reasonable by most participants. However, the extreme sensitivity of the model to changes in the parameters of the relationships

derived from these hypotheses suggests that a careful review of both would be warranted.

Winter mortality and predation mortality are not compensatory. This hypothesis implies that the winter survival rates of deer remaining after predation and hunting are independent of predation and hunting mortality. This hypothesis is invalid if predators take the weaker members of a prey population. Higher predation rates should decrease the number of weaker animals entering the winter and consequently increase winter survival.

9.5 Elk

9.5.1 Effects of Snow

The metabolic costs of a population moving through snow are related only to the depth of snow and the population size. In fact small elk use trails generated by larger elk and the metabolic costs to the population are therefore not simply multiplicative. Also, the type of snow is probably important. Metabolic costs of walking on snow that has a thick ice layer are probably lower than walking on snow without such a layer. The importance of field-testing this hypothesis can be estimated by gaming with the present model. The metabolic cost multiplier for snow (Figure 6.3) can be applied only to adult age classes, or can be scaled up or down to simulate the effects of different snow types.

9.5.2 Movement

The arguments pertaining to deer movement (Section 9.4.2) apply to elk as well. Experiments to accurately define the environmental criteria elk use in choosing habitat would be difficult to conceive and design, let alone undertake. Perturbation studies offer perhaps the best method of discerning the important criteria elk use. Stands of various types could be altered in specific and well-defined ways and changes in the use of those stands by elk measured.

Elk use of an area with snow is only proportional to the available forage in the area. The higher metabolic costs of moving through snow are not "traded off" against forage value. Elk probably utilize a site on the basis of its net energy value. They likely do not use a site with snow simply because it has a high forage value but "compare" the potential energy gains to be made by grazing on the available forage with the metabolic costs of moving through the snow in that site.

Forage under snow is completely unavailable to elk. This is probably not true. Elk may dig under the snow for forage, thereby reducing potential food stress during the winter. Metabolic costs to elk from such activity are likely increased, however (Walters et al., 1975).

9.5.3 Escape Cover

Elk will not use sites with no access to adequate cover. This may be true under conditions of adequate forage availability but may not be true if forage becomes limiting. Under food stress elk may tradeoff the risks of being killed by

predators with the risks of starvation and will feed in areas without good escape cover.

Elk perceive escape cover only in terms of density and height of timber. Other components of habitat are probably also used. Debris and other vegetation may be used by elk, especially the smaller animals. It is probably impossible to derive a good definition of escape cover in a field study. Simply observing where elk spend time is not adequate because elk select habitat using other criteria. Also, escape cover cannot be defined in terms of visibility to humans, as Thomas et al. (1979) have done, but in terms of probability of attack by predators, a difficult quantity to measure. An alternate approach would be to test model behaviour using different definitions of escape cover (i.e., combination of timber attributes, debris, and vegetation).

9.5.4 Forage

Food preferences reflect food requirements. This hypothesis assumes that the forage species selected by elk reflect physiological needs. Therefore, elk would go hungry and suffer decreased survivorship and fecundity if restricted to unpreferred browse. An alternate hypothesis is that elk have "psychological" preferences and suffer no adverse effects if forced to feed on "less preferred" forage types.

This can probably be tested by a review of the literature or by a simple field study in which the physiological status of elk were monitored under different diets.

9.5.5 Emigration

Elk emigrate as a result of perceived elk densities and not as a result of reduced range values. Elk dispersal is presently assumed to be dependent only on population size. This implies that a population will starve at low densities rather than emigrate from a low productivity watershed. Conversely, at high densities, elk will leave very productive ranges. An alternate hypothesis is that emigration is determined by population vigor, as measured by weight, relative forage intake, or some other indicator.

These hypotheses would be difficult to test well in the field because it would entail a large scale experiment. Some indication of what triggers emigration in elk could be dervied, though, by tracking animals with varying physiological states. Presumably, if the former hypothesis is not invalid, movement should be independent of animal vigor; if the latter hypothesis is not invalid, movement will be dependent on animal vigor.

9.6 Predation and Hunting

The effects of predation and hunting in the model appear to be so significant that they mask the effects of forest management practices on wildlife populations. This model result corresponds well with the observations of some participants of dramatic declines in deer populations on Vancouver Island with accompanied influxes and increases in wolves. Given the dramatic effect of predation on wildlife populations, both simulated and real, close investigation of predation on deer and elk is warranted.

9.6.1 Functional Responses

Fawn mortality from bear predation increases as fawn density decreases.

Elk mortality fron cougar predation increases as elk density decreases.

Deer mortality from cougar predation increases as deer density decreases and becomes constant when deer density becomes sufficiently low.

Deer mortality from wolf predation increases to a maximum as deer densities increase from very low levels and decreases with further increases in deer density.

Wolves switch to elk as prey when deer densities decrease to very low levels.

These hypotheses have very different implications for the population dynamics of deer and elk. They imply that, alone, bears have the potential to drive deer populations extinct, cougars have the potential to drive elk populations extinct, while wolves can drive deer populations to very low levels and maintain them at low levels.

The form of the bear functional response and the cougar functional response implies that they have no handling time (time taken to hunt, capture, eat, and digest a prey) when hunting for these prey (Holling, 1959), an invalid assumption. Also, the parameter estimates for the functional responses, such as maximum consumption rates, were "best guess" estimates. The functional responses of the predators should be examined closely.

The functional responses of bear and cougar probably have a form similar to that hypothesized for wolves. All three predator species are generalized. They have a variety of species as potential prey, and take advantage of a particular prey item when it becomes more abundant. Exact determination of the functional response is therefore not practical because alternate prey, as well as deer and elk, would have to be identified and censused. However, it would be useful to estimate the parameters of the functional response (Section 8.2.5.9) under a range of prey densities. They can be derived by visual observations of wolves, bear, and cougar preying on deer and elk (e.g., Haber, 1977). The results may be tempered by the confounding effect of escape cover but will certainly provide a better understanding of the effects of predation.

9.6.2 Numerical Responses

Bear and cougar populations are independent of deer and elk populations.

Wolf populations are independent of elk populations.

Wolves have a numerical response to deer populations.

Numerical responses are difficult to estimate and their estimation may be outside the scope of this program. Predator density estimates on Vancouver Island, coupled with a knowledge of the functional responses, would give a good predictive ability of the potential effects of predators on deer and elk populations.

A review of the appropriate literature would probably give insight into numerical responses. For example, Haber (1976) has found that the numerical response of wolves in the arctic is closely related to changes in the social structure and territory size under different prey densities. Information of this type may be useful to the IWIFR program.

9.6.3 Escape Cover

The presence of escape cover makes a proportion of the prey population "immune" from predation.

Escape cover may affect predation by increasing handling time, decreasing the rate of successful search, or may affect any combination of parameters. The sensitivity of various assumptions about what constitutes escape cover and the effects of escape cover on the functional response should be tested with the present model. The assumptions to which the model is most sensitive can then be tested for in the field. Exploration with the model is a necessary prerequisite because of the likely difficulty in conducting field experiments on escape cover (Section 9.5.2).

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APPENDIX - COMMENTS OF WORKSHOP PARTICIPANTS ON THE DRAFT REPORT

Vegetation Submodel

Arboreal Lichens, p.18, Sec. 3.4

Lichens need light and after thinning,with more light, lichen growth should be greater.

Forage Available for Browsing, p.21, Sec. 3.5

Forage species physical availability is probably 75% - 90%.

Fertilization, p.21, Sec. 3.7

The response to fertilization is dependant on forest density. If the forest is thinned, the assumption holds. If the forest is unthinned, the assumption is false, as the tree canopy will be greatly increased in density with fertilization, shading out the forage.

Effects of Silvicultural Practices, p.88, Sec. 8.2.1.3

Species composition will change with silvicultural practices, as will nutrient levels and palatability.

Managed stands cannot be equated to natural stands which will tend to have a higher live crown ratio.

Alternate Representation of Vegetation, p.88, Sec. 8.2.1.4

It is very difficult to simplify as there are, in reality, scores of habitats which result in significant changes in vegetation. Vegetation also is dependant on overstory density due to tolerance to shading of some species. Micro and macro climate must be considered in vegetation groupings.

There is no more consistency of value as food or of response to management within physiognomic categories than between these categories. These relationships are complex. Too much aggregation takes the result too far from the real world.

Vegetation, p.118, Sec. 8.4.1

On the contrary, food has to be limiting.

Competition, p.125, Sec. 9.2.1

Also, the effect of forest development on forage production and availability must be considered.

Timber Submodel

Changes in Growth, p.25, Sec. 4.1.1.2

If repeated for years, heavy browsing will substantially influence stand development and yield.

Height, p.27, Sec. 4.2

Very dense understory certainly affects tree growth.

Growth, p.70, Sec. 8.2.2.1.2

Browsing, via stem deformation, can cause value losses in the bottom of a tree, but the relationship is basically a growth retardation situation. Heavily browsed trees often grow dramatically once the leaders get beyond reach.

Permanent damage to stem form is unlikely unless we measure limbyness as a result of lower density due to browsing.

Direct Effects of Wildlife p.90, Sec. 8.2.2.2

Effects are usually random affecting single stems, not the entire stand.

Low priority. The usual densities of deer and elk aren't great enough to cause trampling losses.

Effects of Silvicultural Practices, p. 92, Sec. 8.2.2.3

Spacing and thinning may change nutrient cycling thereby changing the quality of vegetation.

Influence of Other Vegetation on Timber, p.92, Sec. 8.2.2.5

This happens at an early age, when seedlings and competing vegetation are at the same root depth.

Not on forest lands. Foresters will get rid of brush quickly if herbicides are available.

Competition from Other Vegetation, p.127, Sec. 9.3.3

Juvenile spaced stands with heavy understory respond very slowly to spacing as the understory is more capable of rapidly spreading to occupy the site and use the additional water and nutrients.

Deer Submodel

Snow Reaching the Canopy, p.33, Sec. 5.1

Accummulation and ablation processes are important because they can change the amount of food available to ungulates.

Snow Reaching the Ground, p.35, Sec. 5.1.2

Fig. 5.1 is not true; even when crown closure is 1, branches eventually bend, snow slides off and reaches the ground.

A crown can hold only a certain amount of snow (mass) before it either slides down or breaks the tree. It depends on the quality of the snow too.

Food Covered by Snow, p.35, Sec. 5.1.3

Improvements could be made by expressing the relationship as non-linear curves. Thus threshold depths could be identified. We used a uniform distribution because the programmer thought it too difficult to use non-linear relationships.

They do move during winter, but we don't know what triggers movements.

Snow Interception, p.93, Sec. 8.2.3.1.1

Wind also strongly affects snow through fall and depth patterns.

Snow quality is important too.

It is important to recognize that winter range must have snow interception.

Movement, p.94, Sec. 8.2.3.2

If movements are to be made more sensitive to snow then the snow model must be run on a daily basis.

Feeding, p.96, Sec. 8.2.3.3

Depending on availability, preferences change markedly.

Survival and Reproduction, p.97, Sec. 8.2.3.4

Deer condition entering winter range is dependant on food quality on summer range. Reproductive success is also dependant on summer range quality.

Snow, p.127, Sec. 9.4.1

The effect of snowfall on food may be fairly easily tested in the field. Sequence and processes of accummulation and ablation can determine the rate at which food becomes buried and the duration of the burial.

Survival and Reproduction, p.131, Sec. 9.4.4

Or, winter conditions may weaken deer and result in even greater predation rates.

Elk Submodel

Escape Cover, p. 97, Sec. 8.2.4.1

Research shows clearly a "marked distance from cover/feeding use" relationship. After about 600 ft. from cover, little use is made of forage.

Visibility is a starting point - it works for escape from humans.

Effects of Snow, p.131, Sec. 9.5.1

Small elk may have easier trails but they end up with food that has been left over by the large elk. It may be of poorer quality than that obtained by the large elk.

Emigration, p.134, Sec. 9.5.5

Competition for available food and lowered food quality on crowded ranges are certainly reasons for movement by other members of the genus Cervus.

Predation and Hunting Submodel

Functional Responses, p.135, Sec. 9.6.1

Presumably the more fawns, the greater likelihood of a bear finding some.

Numerical Responses, p.136, Sec. 9.6.2

Cougar density is probably dependant on elk populations because they are strict carnivores. Bear are omnivorous and only opportunistic carnivores.

If either a numerical or functional response is to be described, one must also estimate deer densities.